

Review Article

Listeria monocytogenes in Livestock and Derived Food-Products: Insights from Antibiotic-Resistant Prevalence and Genomic Analysis

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Abstract

Antibiotics play an important role in veterinary medicine and serve as important tools to maintain animal health and ensure food safety. However, heavy use of antibiotics in animal production can lead to increased antimicrobial resistance from livestock to humans. Foodborne pathogens are a major public health and food safety problem. *Listeria monocytogenes* cause severe diseases and outbreaks associated to the consumption of contaminated food products, in humans. In the treatment of infections, *L. monocytogenes* are susceptible to several antimicrobial agents, however, several recent studies have already reported cases of strains resistant to several classes of antibiotics, such as ampicillin, cefotaxime, tetracyclines, sulfonamides, β -lactams, and penicillin among livestock animals, but also the emergence of multi-resistant strains in these environments have also been described in several recent studies. This review focuses on the occurrence and prevalence *L. monocytogenes* in livestock and derived food-products and strives to provide information on prevalence of *L. monocytogenes* in livestock animals, and derived food products, and describe the main antimicrobial resistance and genomic analysis in strains associated and isolated from regions worldwide.

Keywords: Antibiotic resistance; Foodborne pathogens; *L. monocytogenes*; Livestock; Derived food-products

Introduction

Listeria spp. is a non-spore forming, small Gram-positive rod-shaped bacteria belonging to the phylum Firmicutes, class Bacilli, order Bacillales, family *Listeriaceae*. They are facultatively anaerobe microorganisms, [1-3] and are actively motile, capable of prospering at low temperatures and in severe conditions [4]. They can tolerate salt conditions (NaCl) up to 20% [w/v], grow in a pH range of 4.4-9.6, and thrive in various extreme environmental conditions [1,2] and different environmental niches such as humans, farms, animals, food, food-processing environments, plants, soils, water, silage and sewage [5]. They can survive in water environments and exhibit optimal growth at values around 0.97. They can persist for extended periods at even lower values. such as 0.83 [2]. To distinguish the *Listeria spp.* a variety of tests need to be carried out, including hemolysis, mannitol with acid production, D-xylose, L-rhamnose, and alpha-methyl-D-mannoside [2].

Listeria is a genus of 28 species of ubiquitous bacteria in different niches [1]. It is grouped into two groups: “*Listeria sensu lato*” and “*Listeria sensu stricto*”. “*Listeria sensu stricto*” includes *L. monocytogenes*, *L. innocua*, *L. seeligerii*, *L. welshimeri*, and *L. marthii*. These species are catalase-positive, motile at 30°C, and grow below or at 4°C. “*Listeria sensu lato*” includes *L. grayi*, *L. fleischmannii*, *L. floridensis*, *L. aquatica*, *L. newyorkensis*, *L. cornellensis*, *L. rocourtiae*, *L. weihenstephanensis*, *L. grandensis*, *L. riparia*, and *L. booriae* [1,6]. Among these species, *L. monocytogenes* and *L. ivanovii* are considered the most pathogenic species, and *L. monocytogenes* is responsible for several outbreaks in humans and animals [3,4].

Listeria monocytogenes, first described and isolated by G. Hülphers in 1919, was later identified by E.G.D. Murray in 1923 and J.H. Pirie in 1925. In 1940, it was recognized as *L. monocytogenes* [1,7,8]. Nyfeldt first isolated it in humans in 1929 and later described the circling diseases caused by it in sheep [1]. Listeriosis is characterized as a zoonotic disease resulting from the ingestion of contaminated food by *L. monocytogenes*. Systemic dissemination of pathogens from the gastrointestinal tract depends on their ability to overcome barriers such as the intestinal, blood-brain, and placental barriers [1,9]. Listeriosis is characterized by sepsis and central nervous system infections, occurring primarily in immunocompromised hosts, the elderly, and pregnant women, as well as localized infections anatomically rare. Gastroenteritis is caused by healthy individuals when the ingested contaminated ready-to-eat foods such as hotdogs, cheeses (unpasteurised milk), smoked fish, ice cream, patés, cantaloupe, apple, and vegetables [9,10]. Although morbidity is very low in the normal population, these epidemics are characterized by high hospitalization and mortality rates, especially in high-risk groups with hospitalization rates higher than 95% in these cases [1,10]. This microorganism is responsible for 1600

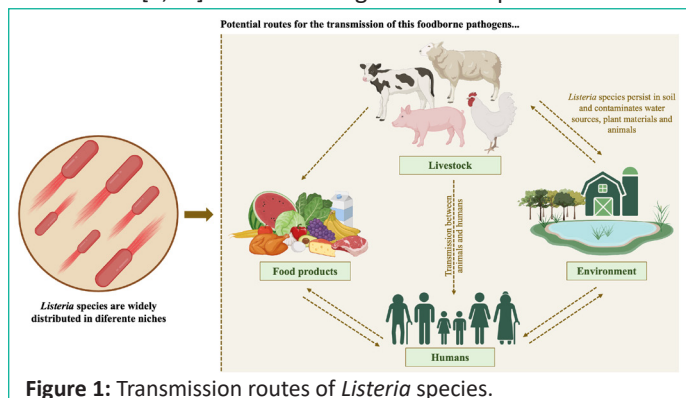


Figure 1: Transmission routes of *Listeria* species.

illnesses and 260 deaths annually in the United States, has a zero-tolerance policy due to its higher disease severity [11]. *Listeria* species, more specific *L. monocytogenes* is a ubiquitous bacterium (Figure 1) known for its adaptability, including antibiotic resistance genes and biofilm formation [2,10]. Its resistance to adverse environmental conditions such as high salt concentration, temperature range low pH and oxygen-limiting conditions, allows it to spread through food and multiply on various surfaces [9].

Prevalence and Occurrence in Livestock

In this review article, we gathered information resulting mainly from studies that detected *Listeria* species in livestock animals, such as goats, cattle, buffaloes, sheeps, cows, dairy cattle, chickens, slaughterhouses, poultry farms and pigs are summarized in Table 1.

Table 1: Prevalence of *Listeria* species reported livestock animals.

Location	Listeria Species	Livestock animals	Sample origin	Collected samples	Prevalence (%)	Reference
India	<i>L. monocytogenes</i>	Goat	Faecal	95	3.15	[80]
			Nasal		6.3	
			Vaginal		3.1	
Latvia	<i>L. monocytogenes</i> <i>L. innocua</i> <i>L. seeligeri</i> <i>L. ivanovii</i>	Cattle	Faecal	111	25.2	[16]
					33.2	
					15.3	
					2.7	
Egypt	<i>L. monocytogenes</i> <i>L. ivanovii</i> <i>L. innocua</i> <i>L. grayi</i>	Cattle	Faecal	70	4.3	
					5.7	
					2.9	
					5.7	
	<i>L. ivanovii</i> <i>L. innocua</i> <i>L. grayi</i>	Buffaloes	Faecal	30	6.7	
					3.3	
					6.7	
	<i>L. monocytogenes</i> <i>L. ivanovii</i> <i>L. innocua</i> <i>L. grayi</i> <i>L. ivanovii</i> <i>L. innocua</i>	Sheep	Faecal	50	8.0	
					6.0	
					2.0	
2.0						
2.0						
<i>L. monocytogenes</i> <i>L. innocua</i> <i>L. ivanovii</i>	Goats	Faecal	25	8.0		
				4.0		
				4.0		
Turkey	<i>L. monocytogenes</i> <i>L. innocua</i> <i>L. ivanovii</i>	Cows	Milk	68	4.41	[13]
					10.29	
					4.41	
	<i>L. monocytogenes</i>	Slaughterhouse A	Chicken	11	0	[55]
		Slaughterhouse B	Chicken	12	16.7	
Norway	<i>L. monocytogenes</i>	Dairy cattle	Faecal	99	30	[22]
Spain	<i>L. monocytogenes</i>	Dairy Cattle	Faecal	79	65	[81]
Italy	<i>L. monocytogenes</i>	Broiler chicken meat	Neck skin	520	26.7	[82]
Canada	<i>L. monocytogenes</i>	Swine meat	Slaughterhouses A Slaughterhouses B Slaughterhouses C Slaughterhouses D	624	9.3	[83]
					8.8	
					15.7	
					5.1	
USA	<i>L. monocytogenes</i>	Dairy cattle	Manure	67	13.1	[56]
		Poultry	Poultry farms	Faecal	1537	
Nigeria	<i>L. monocytogenes</i> <i>L. ivanovii</i> <i>L. grayi</i> <i>L. innocua</i>	Broiler chickens	Faecal	114	13.2	[65]
					7.9	
					2.6	
Germany	<i>L. monocytogenes</i> <i>L. innocua</i>	Slaughter pigs	Tonsil	430	1.6	[19]
					1.2	

Listeria species are widely disseminated in the environmental, but infection in farm animals can occur when grazing on contaminated fields or fields fertilized with contaminated manure [12,13]. Contaminated food and livestock are the source of many foodborne pathogens, and *L. monocytogenes* has been documented in a broad range of animal species, but commonly affect livestock animals and is responsible for listeriosis in animals and humans [14,15]. *L. ivanovii*, also is associated with animal infections and are found to be the most pathogenic along with *L. monocytogenes* [16]. Infections caused by *Listeria spp.* have a negative impact on the livestock economy as well as the food processing industry, including human health [12].

Regarding the prevalence of *Listeria spp.* found in the livestock environment, five *Listeria* species have been identified namely *L. monocytogenes*, *L. innocua*, *L. seeligeri* and *L. ivanovii* has been isolated from all types of samples such as faecal, nasal, vaginal, milk, skins, meat, manure and tosil. *L. monocytogenes* showed the highest prevalence and was isolated in most studies in Table 1. According to Castro et al. (2018), dairy cattle farms have been identified as significant reservoirs of *L. monocytogenes* genotypes associated with human listeriosis outbreaks [14]. However, there are other causes for these contaminations and transmission of *L. monocytogenes* to the farm environment from a multitude of sources, like poor-quality silage [17].

The prevalence of *Listeria spp.* infection in bovine/cattle farm environments is often high, including subtypes associated with human infections and foodborne outbreaks, mainly detected in feces and feeding units [18]. In Table 1, is possible to observe six studies related on bovine/cattle farming in various regions of the world such as Latvia, Egypt, Turkey, Norway, Spain and US, showing rates of *Listeria spp.* infection ranging from 65% to 2%. The presence of different species has also been confirmed., with *L. innocua* being the most common in Turkey and Latvia, followed by *L. monocytogenes* in Norway and Spain. The prevalence rate in the USA was 13% and the prevalence of *Listeria spp.* in cattle environments confirms that this is an important reservoir of the species. Livestock likely spread pathogens asymptotically, showing no signs of illness or shedding bacteria into the farm environment [16].

In pig production, the main problem caused by this pathogenic bacteria is the fact that animals can carry the bacteria without showing any signs of disease at slaughter, leading to direct contamination of carcasses and meat at the slaughterhouse [14,18]. The study in Germany found low prevalence of *Listeria* species, with 1.6% for *L. monocytogenes* and 1.6% for *L. innocua*. However, it suggests that tonsil samples can harbor these species, potentially posing a risk of cross-contamination and food chain spread [19].

In avian farms (chickens, turkeys, waterfowl, geese, ducks, game birds, pigeons, parrots, etc.), the *Listeria spp.* outbreaks are rare and are more frequently reported as an opportunistic pathogen, however, are important potential vectors for contamination of the processing environment. Sporadic cases of listeriosis have been attributed to poultry, indicating that poultry can serve as a potential source of *Listeria spp.* infection in humans. *Listeria spp.* have been isolated from various stages of the poultry production and processing continuum [14,20]. Although, as described, this bacterium is not common in poultry, we can see six studies in our Table 1 in which *Listeria spp.* was isolated from different sources, such as manure, faecal and meat samples. The most common species is *L. monocytogenes* with a prevalence ranging from 27% and 0%. Other three spe-

cies were also detected in the study carried out in Nigeria [21], namely *L. ivanovii*, *L. grayi* and *L. innocua*, with low prevalence.

Improper hygienic practices are strongly associated with the presence of this species in livestock, suggesting that good hygiene is not the only important factor in livestock and that the majority contamination comes from animal and environmental sources. Therefore, all the implementing measures established in farms and their surroundings at every stage of production are of critical importance to have a significant impact in food safety in the future [14,16,22].

Antimicrobial Resistance in *L. monocytogenes*: Emerging Crisis

Antimicrobial resistance is an emerging threat to public health and the development of antibiotic resistance in bacteria has been associated to the use and misuse of antimicrobial in human health and veterinary [23,24]. The use of antibiotics in food animals is common and has been used on a large scale for long periods of time. As a result, a positive selection of resistant bacterial clones can spread to humans through the food chain, with bacteria acquiring a wide variety of antibiotic resistance genes. Commensal organisms found in food or in the gastrointestinal tract of animals and humans that can be a possible way of contamination for *Listeria spp.* and other pathogens [23,25].

Therapeutic options including the use of β -lactam (penicillin or ampicillin) or in combination with an aminoglycoside, mainly gentamicin and amoxicillin [26,27], are the antibiotics selected in the treatment of severe infections or if the patient is allergic to β -lactams. In the case of resistance to the antibiotics like fluoroquinolones, macrolides and tetracyclines, trimethoprim-sulfamethoxazole are successfully used to treat listeriosis [10,26]. The use of antibiotics in human medicine, veterinary medicine, and agriculture actually plays an important role in the emergence and spread of antibiotic resistance [28]. In livestock, veterinarians, and farmers play an important role in the use of antibiotics. Antibiotics are often used both therapeutically and sub therapeutically for the treatment and prevention (prophylaxis) of bacterial diseases in animals [29–31]. The use of antimicrobials at industrial scale for growth promotion purposes in animal agriculture has been a significant concern. Since 2006, European Union (EU) countries and World Organisation for Animal Health (WOAH) banned the use of antimicrobial as growth promoters in animal feed and is believed that the use of antimicrobials is one of the major contributor to the global trend of antimicrobial resistance since they have been used for at least 50 years [28,30,32].

In fact, β -lactams, tetracyclines, aminoglycosides, lincosamides, quinolones, polypeptides, amphenicols, macrolides, and sulfonamides are indeed among the most commonly used classes of antibiotics in food animal production [33]. For cattle, poultry, and pigs, the estimated average annual consumption of antimicrobials is 45 mg/kg, 148 mg/kg, and 172 mg/kg, respectively. Global antibiotic consumption is projected to increase, estimated to increase from 63,151 \pm 1,560 tons to 105,596 \pm 3,605 tons by 2030 [32]. Predictable patterns of intensification in food systems often correlate with increased demand for antimicrobial use [31,33]. As a result, bacteria present in food animals often proliferate in fresh meat and milk and dairy products and can act as a reservoir for resistance genes that can be transferred to humans [32,33]. The first case of antibiotic resistance in a food animal was reported after streptomycin was administered to turkeys in 1951. As a result, widespread resistance to

Table 2: Antimicrobial resistance and genomic analysis of *L. monocytogenes* in different regions.

Location	Animals	Number of isolates	Antimicrobial resistance			Genomic analysis					Reference							
			Method	Antibiotics	Resistance, %	Antimicrobial genes detected	Method	MLST										
								Lineage (%)	ST	CC								
Jordan	Cattle Sheep Goat	32	Disk diffusion	Ampicillin	96.9	-	-	-	-	-	[51]							
				Clindamycin	96.9													
				Penicillin	93.8													
				Erythromycin	93.8													
				Quinupristin/dalfopristin	87.5													
				Streptomycin	75.8													
				Teicoplanin	75.0													
				Linezolid	75.0													
				Vancomycin	71.9													
				Kanamycin	71.9													
				Tetracycline	71.9													
				Gentamicin	50.0													
				Chloramphenicol	43.8													
Ceftriaxone	34.4																	
Ciprofloxacin	15.6																	
Morocco	Raw bovine meat	1	Disk diffusion	Amoxicillin/clavulanic acid	-	-	-	-	-	[52]								
	Raw poultry meat	1		Amoxicillin/clavulanic acid	-													
				Erythromycin	-													
	Raw beef meat	10		Ampicillin	80					-	-	-	-	-	[53]			
				Penicillin	50													
				Amoxicillin	100													
				Sulfamethoxazole	20													
				Sulfamethoxazole/trimethoprim	30													
				Gentamicin	10													
				Streptomycin	50													
Kanamycin	10																	
Tetracycline	50																	
Chloramphenicol	10																	
Erythromycin	50																	
Vancomycin	50																	
Spain	Meat and dairy products	7	Microdilution	Clindamycin	90	<i>tet M</i>	PCR	-	-	-	[23]							
				Tetracycline	30													
				Ciprofloxacin	26													
				Ampicillin	16													
				Penicillin	10													
				Gentamycin	2													
Australia	Dairy products and Meat products	100	Disk diffusion and microdilution	Ciprofloxacin	2.1	<i>fosX, lmrB, ermB, fepR</i>	PCR	Lineage II, (56%) Lineage I(43%), Lineage III (1%)	-	CC1	[85]							
				Erythromycin	1													
Brazil	Lairage, slaughtering and cutting room	16	Disk diffusion	Kanamycin	6.2	-	PCR	-	-	-	[64]							
				Clindamycin	31.2													
				Tetracycline	6.2													
				Erythromycin	6.2													
				Ampicillin	6.2													
				Penicillin	100													
Sulfamethoxazole-trimethoprim	18.6.2 75																	
South Africa	Raw milk	2	Disk diffusion	Sulfamethoxazole	71.43	<i>blaTEM, blaSHV, blaZ, tetA, tetD, tetG, tetM, tetK, aph(3)-IIa (aphA2)a, sul1, sul2</i>	PCR	-	-	-	[86]							
	milk/fresh milk	7																
	Cheese	12										Trimethoprim	52.86					
												Erythromycin	42.86					
											Cefotetan	42.86						
	Ready-to-eat products	6									Oxytetracycline	42.86						
											-	-	<i>EmrB/QacA, Bcr/CflA, SugE, Tn6188, bcrABC, fosX, tetA, tetM, mecC, mrB, msrA, lde, mdrL.</i>	Data-bases	lineage II and lineage	ST1, ST121, ST204, ST876	-	[68]
											-	-						
	-	-																

Turkey	Poultry Slaughterhouse A	11	Disk diffusion	Sulfamethoxazole/trimethoprim	5	-	PCR	Lineage I (90.26%), Lineage II (5.82%), Lineage III (3.88%)	-	-	[55]
	Poultry Slaughterhouse B	12	Disk diffusion	Penicillin G Erythromycin	3 2	-	PCR	-	-	-	[55]
USA	Dairy Manure	58	Broth microdilution method	Ampicillin Penicillin G Chloramphenicol	89.5 47.7 61.7	<i>Lde, ampC, aadB, penA, ermB, tet(O)</i>	PCR	-	-	-	[56]
	Poultry Manure	9	Broth microdilution method	Ciprofloxacin Nalidixic acid Kanamycin	79 95.5 88						
	Manure	47		Gentamycin Streptomycin Tetracycline	77.6 98.5 34.3						
	Soil	20		Erythromycin Azithromycin Ceftriaxone Ceftiofur Trimethoprim/Sulfamethoxazole Meropenem Vancomycin Linezolid Nitrofurantoin Clindamycin Rifampicin Levofloxacin	37.3 100 100 100 100 67 58 8.9 100 100 91						
China	Food (frozen beef, frozen pork, fresh fish, fresh aquatic products, frozen chicken, frozen sheep casing and dairy food products)	101	Microdilution method	Oxacillin Clindamycin Daptomycin Chloramphenicol Tetracycline Ciprofloxacin Erythromycin imipenem	39.33 16.85 6.74 5.62 4.49 3.37 3.37 1.12	<i>aph(4)la, ermC, fexA, tetK, tetM, tetM, tetK; fexA, ermC</i>	PCR	lineage II (64.20 %); lineage I (35.80 %)	ST9, ST121, ST37, ST8, ST1, ST204, ST31, ST59, ST2, ST3, ST4, ST7, ST155, ST21, ST388, ST5, ST6, ST77, ST191, ST2117, ST224, ST26, ST325, ST426, ST451	-	[57]
	Meat products	90	-	-	-	<i>tet(L), tet(M), aph(3')-III, aac(6')-Iaa, str, erm(B), Isa(A), oprA, Cat, fexB, dfrG, sul1, norB, bcrA, aadA3, qnrA2, vanRG</i>	PCR	lineage II and lineage I	ST2, ST9, ST155, ST8, ST121, ST120, ST87, ST196, ST11, ST387, ST705	CC9, CC121, CC155, CC8, CC87, CC2	[58]
Poland	Ready-to-eat products (heat-treated sausages, delicatessen, salads, and packed dinner dishes, Fish seafood.	146	Microbroth dilution method	Oxacillin Clindamycin Ceftriaxone Linezolid Ciprofloxacin Gatifloxacin Gentamycin tetracycline	90.4 54.1 49.3 3.4 0.7 0.7 0.7	-	PCR	-	ST9, ST3, ST580, ST1266, ST1267, ST1268	CC8, CC5, CC9, CC2, CC5, CC8, CC9	[59]
Central Romania	Ready-to-eat processed meat	17	Vitek2 Compact automated system	Benzylpenicillin fusidic acid oxacillin Fosfomycin Clindamycin Imipenem Ciprofloxacin Rifampin trimethoprim-sulfamethoxazole tetracycline	100 100 88.2 82.4 76.5 52.9 41.2 41.2 29.4 29.4	-	PCR	lineage II (58.9%), lineage I (29.4%), lineage III (/11.8)	-	-	[60]

Germany	primary production, processing companies, fresh fruit, frozen berries from supermarkets	8	Broth microdilution	Fosfomycin, cationic peptide, lincomycin, fluoroquinolones	-	<i>fosX, mprF, lin, nor</i>	PCR	lineages I and II (62.5%)	ST1, ST2, ST6, ST7, ST21, ST504, ST1413	CC1, CC2, CC6, CC7, CC21, CC457, CC739	[61]
	Fattening pigs and the slaughterhouse environment	7	Broth microdilution	Clindamycin Pirlimycin	100 100	<i>vga(G), fosX</i>	Bak-Charak pipeline	lineage I and lineage II	ST5, ST6, ST7, ST9, ST18, ST20, ST37, ST325, ST412, ST451	CC5, CC6, CC7, CC9, CC18, CC20, CC37, CC31, CC412, CC11	[62]
Northern Italy	Food sources (beef, dairy, fish, game, mixed food, mixed meat, pork, and poultry)	416	-	-	-	-	-	-	ST1ST2, ST3, ST5, ST9, ST36, ST427, ST663	CC1, CC2, CC3, CC5, CC9, CC36, CC29	[63]
Portugal	Cured Raw Milk Cheese	8	-	-	-	-	-	-	ST788, ST378, ST1, ST9, ST666, ST87	-	[66]

antibiotics such as tetracyclines, sulfonamides, β -lactams, and penicillin, has been observed in a variety of other food-producing animals [32].

Classical microbiological methods and molecular techniques are of great importance for testing *Listeria monocytogenes* in food and manufacturing environments. Molecular-based approaches offer improved discriminatory power for differentiating bacterial strains in epidemiological studies [34]. Whole Genome Sequencing (WGS) technologies are rapidly developing novel typing methods due to their rapid, sensitivity, and high accuracy. They provide extensive additional information, and exhibiting the highest discriminatory power when comparing various organisms, making them effective in detecting foodborne outbreaks and studying pathogenic bacteria molecular epidemiology, including *L. monocytogenes* [35-38]. Analyzing bacterial genome sequences provides detailed information about isolates relationships, molecular types and virulence and resistance markers [36,37,39]. This technology is suitable for national and international surveillance systems, enhancing food safety and public health efforts by understanding infectious diseases epidemiology in the future [39]. The study of lineages and clonal complex is crucial for understanding the relationship between genetic variation within a species and traits like pathogenic potential, virulence, and epidemiology [40]. *L. monocytogenes* exhibits a structured population consisting of 14 serotypes and 4 distinct lineages (I, II III, and IV), which, from an evolutionary perspective, could be regarded as distinct species [41]. Each lineage is characterized by specific serotypes: lineage I includes serotypes 1/2b, 3b, 4b, 4e and 7; lineage II includes serotypes 1/2a, 1/2 c, 3a and 3c; lineage III includes serotypes 4b, 1/2a, 4a and 4c; and lineage IV includes serotypes 4a and 4 c [37,42]. The most predominant serotypes causing clinical infections are 1/2a (lineage II), 1/2b and 4b (lineage I), accounting for over 90% of cases [37]. Notably, serotype 4, belonging to lineage I, is frequently isolated from human infections, indicating its high prevalence and pathogenicity. Serotype 4b is also responsible for a majority of sporadic and outbreak incidents worldwide, further underscoring its elevated pathogenic potential. Strains are organized into Clonal Complexes (CCs) and singletons are Sequence Types (STs) with at least two allelic mismatches [43]. Multilocus Sequence Typing (MLST) can reconstruct ancestral and evolutionary relationships among *L. monocytogenes* isolates and identify all genetic variations within amplified housekeeping genes, which accumulate over time are less common in

human disease, they are frequently found in food and food environments[44]. The lineages are further classified into STs and CCs using Multilocus Sequence Typing (MLST). Lineage I includes the clones CC1, CC2, CC4, and CC6, which are commonly associated with human diseases and dairy products [45], whereas lineage II comprises the clones CC9 and CC121, which are strongly linked to food and food processing environments [41,46].

The monitoring of antimicrobial resistance in zoonotic and commensal bacteria in food-producing animals and food is crucial for several reasons. It helps in understanding the development and spread of antimicrobial resistance. By monitoring resistance patterns, we can identify emerging trends and monitoring provides relevant risk assessment data, and evaluating targeted interventions [23,47]. The first antibiotic-multi-resistant strain (chloramphenicol, erythromycin, streptomycin, and tetracycline) of *L. monocytogenes* was described in France in 1988. Since then, numerous resistant strains have been identified and isolated from both food and human samples. In 1996, antibiotic resistance of *Listeria spp.* was isolated from food products such as cheese and pork [25,48,49]. In response to growing antibiotic resistance in foodborne pathogens, the European Union introduced legislation banning the use of antibiotics as animal feed additives in January 2006 [25]. Multidrug resistance is not a common pattern among *L. monocytogenes*, however, as described is characterized by the ability to develop resistance to antimicrobial agents commonly used in human and animal health. Antimicrobial resistance can occur through various mechanisms, such as target gene mutations (e.g. genes encoding efflux pumps) and the acquisition of genetic elements [49].

There are two main routes for the transmission of antimicrobial resistance between food-producing animals and humans. The first is direct acquisition by contact, which occurs through interaction with food-producing animals or human carriers. A second involves indirect acquisition through the food chain or exposure to an environment with high levels of antimicrobial resistance contamination, such as hospitals, nosocomial acquisition, manure, waste water and agriculture lands [28,50].

Genomic Analysis of *L. Monocytogenes* in Livestock and Derived Food-Products

Table 2 summarizes various studies that investigated the presence of *L. monocytogenes* in livestock and food derived

for detection of antimicrobial resistance and provides an overview of antimicrobial resistance and genomic analysis. A study conducted by Obaidat e Stringer [51] in Jordan analyzed 32 *L. monocytogenes* strains isolated from cattle, sheep and goats and observed a high levels of resistance (95%) to ampicillin, penicillin, clindamycin, erythromycin, quinupristin–dalfopristin (88%) and streptomycin (80)%, with a multidrug-resistant profile. Additionally, more than 70% of the isolates showed resistance to teicoplanin, linezolid, vancomycin, kanamycin, and tetracycline [51]. conducted a study in Morocco [53] and collected and analyzed 520 samples of raw beef bovine and poultry meat. Two *L. monocytogenes* strains were isolated from each sample of raw bovine meat and raw poultry meat. These strains showed high levels of resistance to amoxicillin/clavulanic acid and erythromycin. This study also revealed the presence of virulence factors in *L. monocytogenes* strains recovered from the collected samples [52]. In another study conducted in Morocco [53], 140 raw beef samples were analyzed, and 10 *L. monocytogenes* strains were isolated. The strains were highly resistant to amoxicillin and ampicillin, while moderately resistant to other antibiotics such as streptomycin, penicillin, erythromycin, vancomycin, tetracycline, and sulfamethoxazole/trimethoprim. However, they were highly susceptible to imipenem, amikacin, gentamicin, kanamycin, sulfamethoxazole, and chloramphenicol. Two separate studies on meat and dairy products were conducted in Spain and Australia. Escolar et al. [23] conducted a study in Spain and identified 7 *L. monocytogenes* strains. They showed a general tendency to be resistant or intermediate susceptible to eight of the nine antibiotics tested. The most commonly observed resistance was to clindamycin, with lower levels of resistance were observed to tetracycline, ciprofloxacin, ampicillin, penicillin, and gentamicin [23]. A study conducted in Brazil [54], *L. monocytogenes* in pig slaughterhouse, with resistance most commonly observed to clindamycin, tetracycline, ampicillin and trimethoprim-sulfamethoxazole. The strains exhibiting resistance to all nine antibiotics tested, and showed the highest levels of resistance to these antibiotics, were primarily found in the environment of slaughtered pigs [54]. Limited information is available about antibiotic resistance of *L. monocytogenes* strains isolated from poultry samples. However, a study conducted in Turkey [55] demonstrated low levels of antibiotic resistance among the strains and resistance to sulfamethoxazole/trimethoprim, penicillin G, and erythromycin observed in 5%, 3%, and 2%, respectively [55]. In the USA [56], a study of antimicrobial resistance in dairy cattle and poultry manure, found that 100% of *L. monocytogenes* isolates were resistant to at least one of the tested antimicrobial classes tested. As shown in Table 2, the observed resistance was significantly higher. Among the resistance genes, the prevalence of *penA* (50%), *ampC* (66.6%), and *ermB* (28%) genes was higher than the prevalence reported in other studies [56]. The reviewed studies revealed several patterns and trends related to antibiotic resistance and pathogenic properties of *L. monocytogenes*. Other studies were conducted in different regions of the world, including China [57,58], Poland [59], Central Romania [60], Germany [61,62], and Northern Italy [63]. Evaluation of resistance to various antibiotics was confirmed and the presence of several resistance and virulence genes was confirmed. Analysis of different clonal lineages of the isolates revealed that lineage II was the most common. Regarding STs, several STs corresponding to different clonal complexes were identified. The increase in antibiotic resistance in *L. monocytogenes* highlights the need to monitor the food chain of all food-producing animals and livestock. Widespread use and overuses of antibiotics at various

stages of food production can facilitate the spread of resistant bacteria and multi-drug resistant bacteria that are normally present in the animal production environments and processing chains [64,65].

Multiple studies have been conducted on *L. monocytogenes* strains, employing the WGS as the primary technique. A study conducted in Portugal by Joana Praça et. al [66], in the analysis of ninety-six cured raw milk cheeses from various batches in the Alentejo region of Portugal, the most frequent clonal complexes observed in *L. monocytogenes* typing were ST1, ST9, and ST87, which were detected in five isolates. Interestingly, these three complexes have previously been reported by Alexandra Moura et al. [67] and Anaïs Painset et al. [37] in studies involving clinically confirmed *L. monocytogenes* isolates, as well as in investigations focused on ready-to-eat foods, food-processing environments, and food samples. Moreover, in a study conducted in Spain [68] that identified clinical isolates associated with listeriosis, clonal complexes ST1 and ST87 were also identified as the most prevalent complexes. One study conducted in South Africa [69] isolated six *L. monocytogenes* strains from a ready-to-eat meat product, especially biltong and polony. Four distinct sequence types were identified: ST1, ST121, ST204, and ST876. It was observed that ST1, which was found in 50% of the isolates, has been reported to have a global distribution [69]. Regarding the ST found, ST1 is known to be commonly found in clinical and food isolates across different regions worldwide [70]. ST121 and ST204, on the other hand, are associated with species typically found in food-processing environments. The particular sequence types possess the capacity to endure and persist for extended durations, ranging from months to years, within food-processing environments, thereby continuing to contaminate food products [71,72]. During a study carried out in South Africa [73], *L. monocytogenes* was isolated from various stages of the meat value chain, including different types of meat, meat products, and environmental samples. WGS was employed for characterization purposes and the MLST analysis of the isolated strains revealed the presence of 20 distinct sequence types, primarily belonging to lineages I and II. Among the most prevalent STs identified were ST204, ST321, ST1, ST2 and ST9. It is worth noting that ST204 has been previously associated with strains causing food contamination in meat-related products in studies conducted in France [74] and Australia [75]. However, ST204 has been reported and isolates from various ecological niches, including food processing facilities, non-clinical isolates, and ready-to-eat products. On the other hand, ST1 and ST2 are recognized as the predominant sequence types strongly associated with food contamination and responsible for infections in both humans and animals on a global scale [73]. Some STs (ST2, ST3, ST5, ST9, ST155 and ST204) were found to exhibit mechanisms enabling their survival in animal production environments while also contributing to the persistence of food contamination [73,76]. A study conducted in Latvia [16] examined the genetic diversity of *L. monocytogenes* in cattle farms by analyzing 521 samples collected from 27 cattle farms between 2019 and 2020. Molecular serotyping, Clonal Complexes (CCs), and genetic diversity of the *L. monocytogenes* isolates were investigated. The results revealed that the majority of the sequenced *L. monocytogenes* isolates belonged to serogroup IIa, followed by IVb and IIc. Serogroup IIa was detected in various sources, including soil, feed, water, and animal feces, while IVb was found in water and feces, and IIc was only present in feces. Fifteen ST and corresponding CC were identified among the *L. monocytogenes* isolates. The most abundant STs and CCs were

ST37 (CC37), ST451 (CC11), and ST18 (CC37). In the cattle farms, the predominant STs and CCs were ST18 (CC18), ST37 (CC37), and ST8 (CC8). ST37 was significantly associated with soil and was exclusively observed among soil isolates from for different farms and was linked to ruminants, ruminant farms, and wildlife environments [16,77]. Clonal complexes, CC8, CC11 and CC9, were associated with food and persistence in food-processing environments and had been implicated in listeriosis outbreaks [78,79]. CC37 and CC18 clones suggested adaptation and persistence in the cattle farm environment [16].

The mentioned studies provide valuable insights into the genetic diversity, prevalence, and distribution of *L. monocytogenes* isolates in various settings and geographic regions. The study by Joana Praça et. al [66] in Portugal observed common clonal complexes ST1, ST9, and ST87 in *L. monocytogenes* isolates from raw milk cheeses, which were previously reported in clinical and food related studies. Similarly, in Spain, the same clonal complexes (ST1 and ST87) were found to be prevalent among clinical isolates associated with listeriosis. In South Africa, multiple studies reported the presence of distinct sequence types (ST1, ST121, ST204, ST876) in *L. monocytogenes* strains isolated from ready-to-eat meat products and different stages of the meat value chain.

ST1 was recognized as globally distributed and commonly found in clinical and food isolates. ST121 and ST204 were associated with species prevalent in food-processing environments, capable of persisting and contaminating food products. Furthermore, the study conducted in Latvia, ST37, ST451, and ST18 were frequently identified and the ST8, ST11, ST9, and ST37 were associated with food, persistence in food-processing environments, and ruminant farms. The findings collectively indicate the presence of specific ST and CC that exhibit adaptability, persistence, and potential for food contamination in different ecological niches and highlight the significance of *L. monocytogenes* in various contexts, including food products, clinical infections, food-processing environments, and animal production settings.

Conclusions

The extensive use of antibiotics in human medicine, veterinary medicine, and agriculture has contributed significantly to the emergence and spread of antibiotics resistance. The use of antimicrobials in livestock, particularly for growth promotion purposes, has been a major concern. The presence of antibiotic resistance in food-producing animals, such as cattle, poultry, swines and rabbits, has been well-documented and antibiotics from various classes, including β -lactams, tetracyclines, aminoglycosides, quinolones, and macrolides, are commonly used in food animal production. These antibiotics can lead to the dissemination of antibiotic-resistant bacteria in fresh meat, milk, and dairy products, potentially acting as reservoirs for resistant genes that can be transferred to humans. Studies on *L. monocytogenes* have shown a high prevalence of multidrug resistance strains and exhibit resistance to antibiotics such as ampicillin, penicillin, clindamycin, erythromycin, and tetracycline. To mitigate the spread of antibiotic resistance and ensure food safety, there is a need for surveillance and monitoring of antibiotic use in food-producing animals and the food chain. Responsible antibiotic stewardship practices, strict adherence to regulations, and promoting alternatives to antibiotics in animal agriculture are crucial steps in combating antibiotic resistance. Continued research, including genomic studies using WGS, will play a significant role in understanding and addressing the challenges

posed by antibiotic resistance in foodborne pathogens like *L. monocytogenes*.

Author Statements

Conflict of Interest

The authors state no conflict of interest with respect to the research, authorship, and/or publication of this article.

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Author Contributions

Conceptualization, A.S.; validation, P.P., M.T.R., P.V. and V.F.; investigation, V.S. and A.S.; data curation, V.S., J.E.P., L.C. and L.M.; writing—original draft preparation, A.S., G.I. and V.S.; writing—review and editing, A.S.; All authors have read and agreed to the published version of the manuscript.

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