Food Control 120 (2021) 107540

Contents lists available at ScienceDirect

Food Control

journal homepage: www.elsevier.com/locate/foodcont

Review

Listeria monocytogenes dissemination in farming and primary production: Sources, shedding and control measures

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ARTICLE INFO

Keywords:
Listeria monocytogenes
Farm animals
Dissemination
Control measures

ABSTRACT

Listeria monocytogenes (*L. monocytogenes*) is a well-known pathogenic bacterium that causes the disease listeriosis in both humans and animals. Human transmission mainly occurs via ingestion of contaminated foods and specifically affects pregnant women, newborns, elderly individuals and immunosuppressed individuals. Several outbreaks have been historically associated with the consumption of fresh raw milk and unpasteurized cheese, highlighting the role of good farm hygiene measures to reduce the probability of milk contamination. *L monocytogenes* is ubiquitous in the environment, and therefore, this bacterium is commonly found in silage, haylage, grazing pastures, crop fields, farmyards and even water. Faeces of wild animals, including gulls and rooks, have also been described as important vectors of the pathogen for farm animal contamination, as well as animal bedding, soils or feed bunk tanks, especially when animals are housed during indoor months. Milking lines, including filters, collectors, bulk tanks and other utensils in the room, have been described as important sites of bacterial detection. The ability of *L. monocytogenes* to produce biofilms and to survive in humid environments makes elimination difficult and increases its persistence in equipment and on floors, leading to high risk of milk contamination at harvest in farms. This review explores in depth the different sources of *L. monocytogenes* contamination described in production farms, with a special focus on ruminants, identifying the transmission vectors and analysing the applicable control measures at each stage.

1. Introduction

Listeria monocytogenes (*L. monocytogenes*) is a Gram-positive, facultatively anaerobic, rod-shaped intracellular bacterium that causes listeriosis, affecting both animals and humans. The bacterium is ubiquitous in the environment, and its natural habitat is thought to be decomposing plant material, in which it lives as a saprophyte (Schoder et al., 2012) and can multiply when temperature and humidity are optimal. The genus *Listeria*, family Listeriaceae, currently includes 20 species (LPSN, 2020) that are highly adapted to soil, water and plants (Linke et al., 2014). *L. monocytogenes* has been classified into 3 major well-conserved evolutionary divisions according to serotype, mainly based on the variation in the somatic and flagellar antigens. More than 14 serotypes have been described, with serotype 4 b (division I) being closely associated with human epidemics and serotype 1/2a (division I) being closely associated with contaminated foods (Borucki & Douglas, 2003; Rasmussen et al., 1995).

L. monocytogenes infection has been described in a wide range of animal species, but farm animals are the most commonly affected (Ho et al., 2007). After ingestion, *L. monocytogenes* is able to penetrate the mucosa of the intestine and cause infections in humans and animals, which can include septicaemia, meningitis, encephalitis or uterine infections (Constable et al., 2016; Wiedmann et al., 1997). In animals, encephalitis is characterized by neurological signs (circling, excessive salivation and unilateral facial paralysis). In addition, eye infections, uveitis, and keratitis are also possible (Nightingale et al., 2004). Uterine infections usually lead to abortion, still birth, septicaemia in neonates or subclinical mastitis (Papić et al., 2019). The incidence rate of subclinical mastitis caused by *L. monocytogenes* seems to be lower in comparison with other mastitis pathogens, like *Klebsiella*, *Escherichia-Shigella*,

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https://doi.org/10.1016/j.foodcont.2020.107540
Received 10 June 2020; Received in revised form 3 August 2020; Accepted 4 August 2020
Available online 12 August 2020

Streptococcus or *Corynebacterium*, but its prevalence in farms is high (Pang et al., 2018), Some animals can be latent *L. monocytogenes* carriers without showing any signs of disease. In these apparently healthy animals, the bacterium is frequently found in faeces and in nasal and genital secretions, acting as vectors of infection for the herd.

It has been showed that *L. monocytogenes* can produce chronic intramammary infection in clinical healthy goats, which represents an important bacterium shedding in the farms, and a source of milk contamination (Addis et al., 2019). In cows and sheep with mastitis, *L. monocytogenes* has been detected in their excreted milk and in their quarters and/or udders (Winter et al., 2004). While *L. monocytogenes* haematogenous mammary gland infection has not been ruled out, many studies consider the intramammary route more likely (Bourry et al., 1995; Tzora et al., 1998; Winter et al., 2004). Tzora et al. (1998) showed that intramammary inoculation of L. monocytogenes at levels of 1000 cfu results in a successful colonization and subclinical or mild mastitis. A further study showed how *L. monocytogenes* mastitis is caused by bacteria penetration in the udder through the teat canal (Winter et al., 2004). Therefore, udder faecal contamination is an important source of contamination.

L. monocytogenes is an important foodborne pathogen. Frequently, human exposure can occur through the consumption of raw, unpasteurized milk or cheese, although in the last decade, other foods have also been implicated in several outbreaks, including meatloaf, smoked fish, fermented raw sausages, or vegetables (Acciari et al., 2017; Aksono et al., 2020; Smith et al., 2018). *L. monocytogenes* can also cause zoonoses, albeit with less public health impact, especially in humans in close contact with or with direct exposure to infected herds, faecal particles and dust from which are spread in a windborne manner. The reported infections cause by contact include conjunctivitis and dermatitis with a papular and pustular rash, especially when the infected animals present dystocia and aborted foetuses and are handled without gloves (Constable et al., 2016). However, when infection occurs as a foodborne disease, the outcome can be fatal, especially in immunosuppressed individuals, neonates, elderly individuals and pregnant women. Fortunately, a strong decrease in the incidence of neonatal *L. monocytogenes* meningitis has been detected, probably due to preventive measures in pregnant women (Koopmans et al., 2017). The manifested syndromes include febrile gastroenteritis, septicaemia, abortions and central nervous system infections, such as meningitis, meningoencephalitis and rhombencephalitis (Oevermann et al., 2010).

The seasonality of *L. monocytogenes* in farms and their environments has been previously described, with the bacterium being more prevalent during spring and winter seasons than in fall or summer (Mohammed et al., 2019; Nightingale et al., 2005; Welshimer & Donker-Voet, 1971). In ruminants, several factors associated with the suppression of host immunity have been identified as promoters of infection. Sudden changes in ration, extremely cold weather, overcrowding of animals indoors, prolonged periods of transport, pregnancy, parturition, lactation, or other situations of stress are often linked with listeriosis. Contamination of milk with *L. monocytogenes* is more frequently reported during winter months than in the rest of the year, perhaps due to increased exposure of animals to different sources of infection (Nightingale et al., 2005).

In addition to animal feed, surfaces and materials in close contact with farm animals, including feed bunks, water troughs, and bedding, have been described as important vectors of listeriosis in dairy farms. Furthermore, the great variety of *L. monocytogenes* serotypes found on farms has led to hypotheses regarding the introduction of the bacterium by wild or domestic animals, farm visitors and contaminated vehicles or machines (Castro et al., 2018) (Fig. 1). These findings reveal the need for specific sanitary measures against this bacterium in the immediate

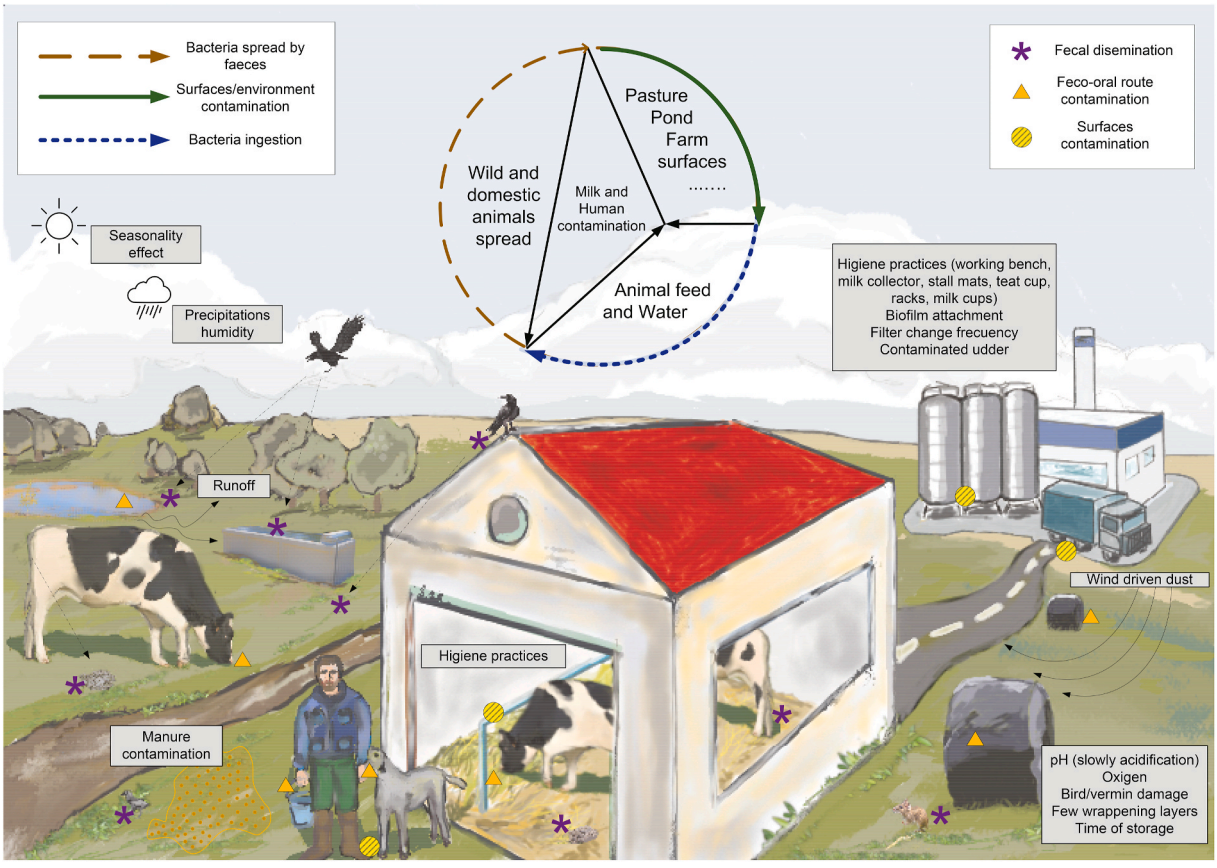

Fig. 1. Graphical abstract of the relationships and interactions between farmers, animals and the environment, potentially leading to *L. monocytogenes* shedding and interspecies transmission.

environments of farm animals (Mohammed et al., 2019). In this review, we investigate the ecology of *L. monocytogenes* on dairy farms and the identification of the main sources of contamination, which are essential factors for improving these control measures.

2. *L. monocytogenes* in food production animals

L. monocytogenes has been identified in almost all common types of animal production, although the most important foodborne outbreaks have been mainly associated with raw milk, unpasteurized milk and other dairy products (Shamloo et al., 2019). Dairy cattle farms harbour *L. monocytogenes* genotypes associated with human listeriosis outbreaks (Castro et al., 2018). Furthermore, these genotypes are also associated with several outbreaks in ruminants, including abortions in cattle (Whitman et al., 2020), encephalitis (Wiedmann et al., 1994), and rhombencephalitis (Dell'Armelina-Rocha et al., 2013). A previous study conducted in dairy cattle did not detect an association between faecal shedding of *L. monocytogenes* and lactation number or lactation day (Ho et al., 2007). Treatment against lice was found to be associated with the presence of *L. monocytogenes* in animal faeces, with up to 56% of animals excreting the bacterium after treatment (Ho et al., 2007). The authors hypothesized that the antiparasitic agent used could be responsible for immunosuppression in animals, as also reported in goats (Tamang et al., 1988). However, in the same study, stress after cattle manipulation was not excluded as a possible co-factor of faecal shedding of the bacterium (Ho et al., 2007).

In pigs, infection by *L. monocytogenes* is relatively unusual, although the bacterium is commonly detected in the faeces of healthy animals, in feed, in litter, on floors and walls, and in feed units. A recent report identified an outbreak of fatal listeriosis in fattening pigs in a piglet-producing farm in Lower Austria. Animals presented bloody and watery diarrhoea, anorexia, increased body temperature up to 40 °C, septicaemia, circulatory insufficiency and fibrino-necrotic typhilocolitis. Poor-quality maize silage contaminated with the bacterium and mycotoxins of *Fusarium sp.* (3000 ppb deoxinivalenol (DON) and 270 ppb zearalenone (ZEA)) was identified as the source of the infection. In this outbreak, the authors hypothesized that the immunosuppression caused by DON could contribute to the persistence and pathogenicity of *L. monocytogenes* in the intestine (Stein et al., 2018). However, the most common problem associated with *Listeria* in swine production is pork product contamination, especially because the animals can be carriers at slaughter without showing any signs of disease. Pigs that harbour *L. monocytogenes* on farms can carry the pathogen into the slaughterhouse and be a direct source of contamination for carcasses and meat at the slaughterhouse and in production plants (Constable et al., 2016; Hellström et al., 2010).

L. monocytogenes is able to infect most avian species (chickens, turkeys, waterfowl, geese, ducks, game birds, pigeons, parrots, etc.), although outbreaks are rare. The bacterium is more frequently reported as an opportunistic pathogen, associated with coccidiosis, infectious coryza, salmonellosis, campylobacteriosis, parasitic infections, etc. (Dhama et al., 2013). Furthermore, grow-out farm studies have shown that avian species are important potential vectors for *L. monocytogenes* contamination of the processing environment (Rothrock et al., 2017).

3. Animal feed as a source of *L. monocytogenes* contamination

Animals exposed to *L. monocytogenes* by feed can contract infection or act as carriers of the bacterium without showing any signs of disease, excreting the bacterium in the faeces (Castro et al., 2018). These animals constitute an important reservoir that must be controlled since faecal contamination during milking can lead to the presence of the bacterium in the bulk tank and therefore in the raw milk. Recently, an important epidemiological link between silage, water sources, subclinical mastitis and *L. monocytogenes* contamination in dairy farms was reported (Papić et al., 2019). It has been shown that the quality of feedstuffs provided (especially during indoor seasons) has a direct influence on the immune status of the animals and therefore on the acquisition of the infection (Nightingale et al., 2005). Poor-quality or poorly preserved silage was identified as a direct source of *L. monocytogenes* contamination in cattle farms (Castro et al., 2018; Nucera et al., 2016). High quality silage is safe for the animal, for the consumer, for the environment, and an excellent feed, as the microbes in properly made and managed silages have probiotic effects on livestock (Driehuis and Elferink, 2000). Well preserved silages are characterized by a rapid acidification, with a final pH ranging between 3.7 and 4.7, in function of the type forage (legume, grass or corn silage), and with an anaerobic atmosphere inside the silo (Limin Kung et al., 2018). When oxygen is available or when the pH is above 4.7, undesirable microorganisms can proliferate and produce hazards to animal or human health. These microorganisms include *L. monocytogenes, Bacillus cereus, C. botulinum,* or even molds with mycotoxins production, among others. Other yeast or butyric acid bacteria are not directly dangerous for animal health, but they produce a reduction in the quality of the silage (Santos et al., 2015).

In sheep and goats, contaminated silage has been reported to be a source of infection and to contribute to massive contamination of the farm and milk processing environment (Schoder et al., 2012). The detection of *L. monocytogenes* seems to be relatively high in herds fed component feed and leftover feed (Constable et al., 2016).

Access to pastures is an important and beneficial practice for animals in terms of physical health, animal welfare and handling. In terms of physical health, cattle in pastures suffer less from lameness, hoof pathologies, hock lesions, mastitis, uterine disease and mortality than confined cattle (Arnott et al., 2017). Animal behaviours, including agonistic, lying or oestrous behaviours, and synchronicity are better in pasture-based cows than in confined cows (Mee & Boyle, 2020). Although the milk production can be somewhat reduced, other economic factors, including labour for animal care, manure handling, forage management, and cow culling rates, also favour outdoor management (White et al., 2002). Furthermore, animals with access to and maintained on pastures are associated with a decreased rate of *L. monocytogenes* faecal shedding (Nightingale et al., 2005), even though the bacterium is ubiquitous in the environment and some factors can lead to its high abundance in grass and other soil samples (Coblentz & Akins, 2018).

3.1. Fermented silage and its impact on listeriosis

Ensilation is a process for conservation of forages in the wet state through acidification, which prevents the continued occurrence of plant life processes and undesirable microbial activity. Unlike haymaking, this process is independent of atmospheric conditions and preserves the humid state through acidification. For good quality and good preservation of silage, rapid acidification by acetic and lactic fermentation and maintenance of anaerobic conditions are necessary (Driehuis and Elferink, 2000). *L. monocytogenes*, which is a part of the normal bacterial composition of grass, can proliferate when there is aerobic spoilage and deterioration of silage during storage or feeding (by hand-tying a perforated bag, with holes made by birds, vermin, etc.) (Coblentz & Akins, 2018; Fenlon, 1986). Big bales of silage are at great risk for *L. monocytogenes* contamination due to the low density and due to the high probability of mechanical damage to the plastic covering (Schoder et al., 2012). To reduce this risk, it is important to use high-quality polyethylene stretch films and to increase the number of wrapping layers to 6 or even 8 (Nucera et al., 2016), and the pH can be checked before use for control of contamination (4/4,5 or below) (Sanaa et al., 1993). A previous study investigated the environmental factors that can directly influence the presence of this bacterium in fermented silages (Pauly & Tham, 2003). In this study *L. monocytogenes* was not detected in untreated silages after 90 days or more, even at a pH of 4.9 or higher. This finding indicates that the time of storage may be one of the most important factors for reducing bacterial counts, which could be

combined with intensive fermentation as an optimal measure to prevent the survival of the bacterium. A further study showed how the silage stored in a bunker was associated with an increased rate of *L. monocytogenes* faecal shedding, while bag storage showed the opposite effect (Nightingale et al., 2005).

Additives such as formic acid or lactic acid bacteria with cellulolytic enzymes had a negative influence on *L. monocytogenes* persistence when applied in wet silages and wilted crops, respectively. Further studies described the effects of bacteriocins produced by *Streptococcus bovis* HC5 or *Pediococcus acidilacti* in maize silages and demonstrated their effectiveness for *L. monocytogenes* control as well as for improvement of the fermentation process (Amado et al., 2016; Mantovani and Russell, 2003). Furthermore, a mathematical model investigated *Listeria* growth in aerobically deteriorated silage bales (Ruxton & Gibson, 1995). The authors found that the puncture size directly affected the increase in pH; small punctures were more harmful when bales were stored for a long time than when bales were stored for a short time.

Several studies have investigated the contamination of feed for milk cows (Table 1). Nucera et al. (2016) detected *L. monocytogenes* in 6 out of 80 (7,5%) silages, with most of the positive samples belonging to mouldy areas. One previous study described that cattle are more exposed to *L. monocytogenes* through contaminated feed than small ruminants. However, it is likely that this continuous exposure improves their immunity to the infection (Nightingale et al., 2004). While feeding with silage is normal on dairy farms, it is not such a frequent practice in calf-cow operations, which seems to explain the relatively low prevalence of the bacterium in these types of farms (Mohammed et al., 2010).

In Europe, the introduction of baled silage was marked by an increase in listeriosis cases in small ruminants (Coblentz & Akins, 2018; McDonald et al., 1991). Grass silage has been described as an important source of listeriosis in sheep (Gronstol, 1979). In clamp silage, the reported prevalence ranged between 2.5 and 5.9%, while in big-bale silages, the percentage of positive samples was between 22.2% and 44%, when the silage had moulds (Fenlon, 1986). Other consequences of silage contamination in ruminants are eye infections and keratitis, linked to direct inoculation of the bacterium in the conjunctiva during intake (Nightingale et al., 2004).

3.2. Pasture, grains and manure

Different environmental factors can influence the natural animal contamination of pasture, grass and silages, and unfortunately, these factors are often the most difficult ones to control. Recently, listeriosis contamination in farm environments was attributed in part to the use of products from wastewater treatment and animal manure in soils to improve their physical and organic properties (Coblentz & Akins, 2018; McDonald et al., 1991). It has been shown that genus *Listeria* is able to survive in both solid manure piles and in slurry samples for several weeks. Furthermore, bacterial viability is related to weather and pile size (Biswas et al., 2018). Different possibilities of treatment methods for manure have been proposed in order to reduce the load of undesirable microorganisms, some of them include: i) composting, ii) aeration, iii) biogas production, iv) chemical disinfection v) pasteurization, vi) lactic acid fermentation and vii) desiccation, among others. (Scheinemann

Table 1
Previous research studies investigating the presence of *L. monocytogenes* in animal feedstuffs and feeding surfaces in ruminant farms.

Type of sample	Animal	Type of production	Geographical localization	Number of farms tested	Prevalence in animal faeces	References
Feeding surfaces	Cattle	Milking cows	Finland	3	25.9% (34/131)	Castro et al. (2018)
Feed bunks			Central New York State	50	65% (158/242)	Mohammed et al. (2009)
		Feedlot operations	Central and southern California	25	2.5% (3/121)	Mohammed et al. (2010)
Cow feed		Feedlot operations	Central and southern California	25	1.7% (118)	Mohammed et al. (2010)
Feed concentrate		Milking cows	Finland	3	16% (4/25)	Castro et al. (2018)
Produced fields	General	Soy bean and corn crops	Hannover Virginia (USA)	12	40% (8/20)	Welshimer, 1968[10]
Feedstuffs (haylage and silage)	Ruminants	Dairy and meat farms	New York State	52	16.8% (87/516)	Nightingale et al., 2004;
Grazing pastures, crop fields and farmyard					23.8% (120/504)	
Cut grass	Cattle	Cow-calf operations	Central and southern California	25	5.3% (n = 132)	Mohammed et al. (2010)
Pasture	Ruminants	Dairy farm	Australia	7	7% (1/14)	MacDade and Hall, 1964
	Cattle	Cow pasture	Burgundy (France)	–	17% (9/53)	Locatelli et al. (2013)
Produced fields	General	Proximity to pastures and grass field	New York State	–	15% (88/588)	Strawn et al. (2013)
		Agricultural fields, soils, animal-inhabited area	India	–	5.4% (7/130)	Moshtaghi et al. (2003)
Cow feed and pasture	Cattle	Dairy farm	Maryland	1	7.1% (1/14)	Pang et al. (2017)
Pasture and pelleted ration			Uruguay	1	20% (1/5)	Matto et al. (2017)
Silage		Milking cows	Central New York State	50	30% (72/240)	Mohammed et al. (2009)
			Finland	3	16.7% (21/126)	Castro et al. (2018)
		Dairy farms	Tennessee	4	6.2% (6/97)	Murinda et al. (2004)
			Japan	20	10% (2/20)	Takai et al. (1990)
		Cows producing milk	Italy	20	7.5% (6/80)	Nucera et al. (2016)
	Sheep	Agricultural environment	Scotland	–	22%–2.5% (clamp/big bales silage) 44% in silages with molds (sheep)	Fenlon et al., 1985
	Small ruminants	Ovine and caprine milking farms	Austria	53	8.6%	Schoder et al. (2011)

et al. (2015); Roberts et al., 2016; Scheinemann et al. (2015); Heinonen-Tanski et al., 2006). However, all of these methods have different technical and hygiene-related limitations, as well as important associated costs (Heinonen-Tanski et al., 2006). Therefore, their use usually depends on the form of manure, the size of the animal unit and the available resources for exploitation. For example, Scheinemann et al. (2015) described how macrobiotic shift during lactic acid fermentation of cow manure or sewage sludge was a low-cost method that inactivated *L. monocytogenes* and other pathogens after 3 days of fermentation, even at 27 °C. Regarding drying treatments, previous studies showed how *L. monocytogenes* is able to survive in manure with a water content less than 30%, although bacterial multiplication is limited (Kim & Jiang, 2010; Himathongkham and Riemann, 1999). This may be due to the inherent resistance to desiccation through the thick peptidoglycan wall possessed by Gram-positive bacteria (Roberts et al., 2016). In this context, potential serotype-specific resistance to desiccation or humidity fluctuations has been described for serotype 1/2 b strains at up to 75% relative humidity (Zoz et al., 2017). Further studies have described how Gram-positive bacteria are more resistant to stress factors than Gram-negative bacteria when they are exposed to unfavourable environmental conditions (MacDade and Hall, 1964; Bale et al., 1993). Different metabolic pathways have been related with the survival of the bacterium in adverse conditions. *L. monocytogenes* is able to grow in osmotically stressful environments using compatible solutes. The bacterium accumulates glycine betaine osmolite intracellularly when grown under osmotic stress, and this accumulation occurs by transport from the medium rather than novo synthesis (Ko et al., 1994). Branched-chain fatty acid also responds to the environmental stress by adjusting membrane fluidity (Zhu et al., 2005). Oxygen limitation in the medium also induces acid tolerance response and survival via the activation of the acid glutamate system (Roberts et al., 2020; Sewell et al., 2015).

The presence of *L. monocytogenes* in treated manure without *Salmonella* contamination has also been described, indicating that Enterobacteriaceae are not the sole indicators of safety in waste treatment (Bonetta et al., 2011). General recommendations that could be applied for all farms are to avoid application of raw animal manure in pastures, lands and crops; to correctly cover the manure to prevent runoff in the environment; to store the manure separately and only by batch; and to introduce anaerobic digestion of waste (Manyi-Loh et al., 2016). Finally, it is necessary to reduce, as much as possible, the microbial load in animals during feeding and breeding, which will have a direct impact on the bacterial levels in excreted animal faeces.

Several studies have investigated the presence of *L. monocytogenes* in animal feed, including pastures, cut-grass and crops. Differences can be observed in relation to the prevalence of this bacterium in soils, but these differences are probably due to a seasonal effect or due to the use of different sampling strategies and culture methods. Pastures are extensive areas in which the presence of bacteria is not evenly distributed and varies strongly depending on the area studied. Regarding culture methods, sensitivity depends on the use of enrichment media or other rapid molecular techniques (Locatelli et al., 2013). A possible seasonal variation in the frequency of bacterial occurrence in soils, with isolation not observed during autumn months, has also been described (Welshimer & Donker-Voet, 1971).

The two first studies carried out in the late sixties and early seventies in Virginia observed the presence of *L. monocytogenes* in soybean crops and in pieces of stalks, leaves and tassels of corn crops, with prevalence ranging between 66.7% and 91.7% (Welshimer, 1968; Welshimer & Donker-Voet, 1971). In the second study, the bacterium was isolated only during the spring collection, suggesting a possible seasonal effect. According to this finding, Nightingale et al. (2005) also reported a seasonal fluctuation in cattle farm soils located in the state of New York, with higher levels of bacteria observed in spring and winter months than in the rest of the year. In livestock farms in Korea, the presence of *L. monocytogenes* was observed in only 3 soils out of 2018 samples tested (0.15%). However, all of the isolates found presented virulence genes and phenotypic resistance to antibiotics (Oh et al., 2016). In French soils, *L. monocytogenes* was reported with a prevalence of 27% only in cow pasture samples, but with levels that did not exceed 10^4 cfu/g (Locatelli et al., 2013). The bacterium was not isolated from cultivated soils, meadows or forest soils, suggesting that cattle also have an important role in the spread and contamination in the environment. In this context, a further investigation showed one case of brainstem encephalitis caused by *L. monocytogenes* in a 2-y-old cross-breed bull, and the source of infection was finally identified as the pasture where the bull grazed. Surprisingly, this pasture had not been previously fertilized with manure or sewage sludge, indicating that the bacterium in the soil originated from cattle faecal shedding (Matto et al., 2017). These findings are consistent with other studies in which authors suggested that cattle are the main source of contamination by faecal deposition during grazing (Mohammed et al., 2010).

4. Birds, wild animals and other environmental factors

The contamination of soils can contribute to the spread of the bacterium through farm animals or other wild animals, which can act as additional important vectors for bacterial transmission (Table 2). The access of birds to feed storage in farms has also been associated with the contamination of cereals, grains and straw (Konosonoka et al., 2012). Wild birds living close to agricultural environments can act as carriers of *L. monocytogenes,* and they can contribute to the spread of bacteria through their faeces in pastures, soils, water and other feedstuffs (Schoder et al., 2012). Seagulls feeding at sewage facilities as well as rooks (but to a lesser extent) have been previously identified as carriers of *L. monocytogenes* in faeces, and their bacterial load is associated with the nesting season and the peak period for listeriosis in sheep (Fenlon, 1986). A previous study investigated the presence of several pathogens in the environments of four dairy farms. The authors revealed the presence of *L. monocytogenes* in bird droppings, mostly in geese, with a prevalence of 10%. However, none of the samples tested from flies, rats and birds were positive for the bacterium, which confirms the fundamental role of birds as vectors of this pathogen (Murinda et al., 2004).

Further studies have highlighted the influence of environmental conditions on the spread of bacteria, especially in mixed farms, where there is a risk of not only crop contamination but also of contamination of grass destined for fermentation to be converted to silage. Pang et al. (2017) showed that seasonality was not the most important factor for the dissemination of listeria species in soils, but abundant precipitation and high wind speed acted as vectors for pathogen transmission via run-off and windborne dust. A further study found that precipitation and the occurrence of alternating freezing and thawing temperatures before soil sample collection were predictors for the presence of genus *Listeria* (Ivanek et al., 2009). In this context, a prevention strategy could be to postpone mowing if these weather conditions occur in the two days prior to harvest. Moisture also seems to influence the prevalence of *L. monocytogenes* in soils and vegetation, with the bacterium being more prevalent in moist pastures and grassy fields (Strawn et al., 2013). However, even though soil pasture contamination may be a source of contamination (Nightingale et al., 2004), it has been suggested that management systems that include pasture grazing reduce the prevalence of *L. monocytogenes* shedding (Nightingale et al., 2005). This is because although it does occur, exposure occurs less frequently in pastures than when the animals are housed in a stable, in contact with many other potential sources of contamination (Table 2).

5. Water and farm animal environments as sources of *L. monocytogenes* contamination

High farm density during indoor months is an important factor for *L. monocytogenes* shedding and infection in farms. This overcrowding favours the spread of the bacterium between animals and the contamination of several surfaces, including feed bunks, water, and farm soils. In

Table 2
Occurrence of *L. monocytogenes* in farm animal environment: water, bedding, soils, faeces and manure.

Type of sample	Animal	Type of production	Geographical localization	Number of farms tested	Prevalence in animal faeces	References
Water	Ruminants	Dairy and meat farms	New York State	52	19.7% (100/508)	Nightingale et al., 2004;
	Cattle	Dairy farms	Dairy farms	16	17% (6/36)	Fox et al., 2009
Water trough surface		Milking cows	Finland	3	32% (48/150)	Castro et al. (2018)
Water trough		Dairy farms	New York State	1	64.3%	Latorre et al. (2011)
		Milking cows	Central New York State	50	66% (160/242)	Mohammed et al. (2009)
		Cow-calf and feedlot operations	Central and southern California	25	0.8% (n = 121) - 3.1% (n = 32)	Mohammed et al. (2010)
		Milking cows	Finland	3	4.8% (4/83)	Castro et al. (2018)
		Dairy farm	Tennessee	4	1.1% (1/92)	Murinda et al. (2004)
Lagoon cattle					7.4% (7/94)	
Water ponds		Cow-calf operations	Central and southern California	25	6.5% (n = 31)	Mohammed et al. (2010)
	Ruminants	Dairy farm	Australia	7	6.5% (2/31)	MacDade and Hall, 1964
Water tank	Small ruminants	Sheep and lamb's meat farm	Switzerland	1	10% (1/10)	Dreyer et al. (2015)
Water various (including water pipe, water trough, water pond, water household	Cattle	Dairy farm	Slovenia	1	57,1% (4/7)	Papić et al., 2019
Exit point from irrigation ditch		Cow-calf operations	Central and southern California	25	14.3% (n = 15)	Mohammed et al. (2010)
Milking line rinse water		Milking cows	Finland	3	3.1% (1/32)	Castro et al. (2018)
Working bench	Small ruminants	Ovine and caprine milking farms	Austria	53	4.7%	Schoder et al. (2011)
Bedding (sawdust)	Cattle	Milking cows	United Kingdom	44	31.7% (13/44)	Bradley et al. (2018)
Bedding (sand)				41	58.5% (24/41)	
Bedding (recycled manure)				40	15% (6/40)	
Bedding (sand, wood shavings or straw)		Dairy farm	Tennessee	4	14.4% (13/90)	Murinda et al. (2004)
Bedding		Milking cows	Central New York State	50	55% (132/240)	Mohammed et al. (2009)
Bedding in barn	Cattle	Milking cows	Finland	3	23.5% (16/68)	Castro et al. (2018)
Bedding storage					10.4% (5/48)	
Soil	Ruminants	Dairy and meat farms	New York State	52	23.8% (120/504)	Nightingale et al., 2004;
	Cattle	Cow-calf and feedlot operations	Central and southern California	25	0.7% (n = 972) - 5.3% (n = 132)	Mohammed et al. (2010)
	Small ruminants	Sheep and lamb's meat farm	Switzerland		10% (1/10)	Dreyer et al. (2015)
	Cattle and pigs	Livestock (pigs and cattle) farms	Korea	25	0.4% (3/680)	Oh et al. (2016)
	Cattle	Dairy farms	Dairy farms	16	3% (1/35)	Fox et al., 2009
Floor swabs	Small ruminants	Ovine and caprine milking farms	Austria	53	7.9%	Schoder et al. (2011)
Floors in the parlor pit and storage	Cattle	Cow dairy farm	New York State	1	20% (2/10)	Latorre et al. (2011)
Soil (waiting area floor)		Milking cows	Finland	3	56.6% (16/31)	Castro et al. (2018)
Soil (milking room floor)					42.1% (16/38)	
Soil (milking station floor)					47.5% (38/80)	
Wild animals		Cow-calf operations	Central and southern California	25	2.5% (n = 40)	Mohammed et al. (2010)
		Dairy farm	Tennessee	4	10% (2/20)	Murinda et al. (2004)
	General	Agricultural environment	Scotland	–	8.3% (23/275) (gulls) 9.8% (12/123) (rooks)	Fenlon et al., 1985
Fecal slurry/pats	Cattle	Dairy farm	Tennessee	4	14.3% (14/98)	Murinda et al. (2004)
Calf fecal swabs					1.2% (1/86)	
Fecal samples	Ruminants	Dairy and meat farms	New York State	52	20.3% (107/528)	Nightingale et al., 2004;
		Dairy farm	Australia	7	6% (1/16)	MacDade and Hall, 1964
	Cattle	Dairy farms	Dairy farms	16	12% (4/34)	Fox et al., 2009
		Cow dairy farm	New York State	1	6% (57/935)	Latorre et al. (2011)
		Cow-calf and feedlot operations	Central and southern California	25	0.3%–3.7%	Mohammed et al. (2010)

(*continued on next page*)

Table 2 (*continued*)

Type of sample	Animal	Type of production	Geographical localization	Number of farms tested	Prevalence in animal faeces	References
Manure		Feedlots	Australia	5	16%–35%	Klein et al., 2010;
Manure	Cattle	Anaerobic digestion plant	Italy	1	20% (1/5)	Bonetta et al. (2011)

this context, it has been reported that contaminants in cheese-making facilities may come directly from the external farm environment (Fox et al., 2011). Establishing protection zones along surface watercourses, within farms and in buffer zones around farms has been shown to be effective in reducing contamination (FAO, 2020).

5.1. Water and farm soils

Water has been identified as an important source of *L. monocytogenes* contamination in dairy farms. The bacterium was detected in water pipes (barn), water troughs (barn), and water ponds and even in water from household samples and was directly associated with subclinical listerial mastitis, even though the bacterial counts in these samples were low (Papić et al., 2019). A further study showed that the bacterium was present with high prevalence at exit points from irrigation ditches, but its presence at entry points was highly unusual. Therefore, the authors hypothesized that water and water trough contamination in farms probably comes from the animals themselves (Mohammed et al., 2010). In water troughs, the detection of the bacterium has been associated with the presence of biofilms (Latorre et al., 2011).

Previous detection of *L. monocytogenes* in pond and soil samples and its correlation with its in cattle indicates that farm environments are another source of animal contamination (Table 2). In general, the prevalence of the bacterium in soils reaches 6%, being detected frequently in September and in agricultural land and urban environments (Linke et al., 2014). Furthermore, soil contamination in farms probably ends in water ponds, in which a prevalence of *L. monocytogenes* of up to 6.5% has been observed (Mohammed et al., 2010). During an outbreak that occurred in 2014 in a Swiss sheep-fattening farm, *L. monocytogenes* was detected in soil samples and water tanks, but all of the animal faeces were negative for the bacterium. Furthermore, the environmental contamination disappeared after thorough cleaning of pens and barns. These findings suggested that farm environment hygiene is crucial for the control of *Listeria* outbreaks (Dreyer et al., 2015). After drinking contaminated water, cattle become vectors for *L. monocytogenes* shedding on the farm and in the environment, perpetuating the bacterial infection cycle (Latorre et al., 2011).

If soils are contaminated with the bacterium, it is not surprising that shoes play a role in bacterial dissemination. The work boots of farmers, veterinarians or visitors have also been described as vectors for *L. monocytogenes* transmission. A previous study isolated genus *Listeria* and *L. monocytogenes* with frequencies of 51% and 15.7%, respectively. The authors also suggested the role of a veterinarian in bacterial transmission among farms based on pulsotype results (Schoder et al., 2012).

5.2. Bedding

The type and microbial contents of bedding have a direct impact on animal health and milk quality. Traditionally, materials used for bedding include sawdust, hay, fresh and recycled bedding sand, calcium carbonate, rubbers and mats. Recently, the use of recycled manure solids obtained by mechanical separation of manure removed from dairy cows' housing systems was also introduced. The characterization of this material has revealed that it can be successfully used without specifically favouring the growth of environmental bacteria compared with other common bedding sources (Husfeldt et al., 2012). A recent study isolated *L. monocytogenes* in higher proportions from sand (up to 58,5%) than from sawdust (31.7%) or recycled manure solid-based (15%) bedding, even though the latter presented significantly higher total bacterial counts. The authors suggested that the high counts of *L. monocytogenes* in sand were due to previous contamination of the soil or to low frequency of bed replenishment, but this contamination could not be related to the presence of the bacterium in milk (Bradley et al., 2018). With regard to bedding residues, the removal of heaps of livestock bedding waste from animal pens to a secondary location with a higher temperature has been described as a simple method for reducing pathogen levels in solid farm wastes (Hutchison et al., 2005).

5.3. Farm surfaces

The existence of persistent niches of *L. monocytogenes* on farm surfaces, including floors, feeding surfaces and water surfaces, has been described, and these niches increase oral exposure to the bacterium (Castro et al., 2018). Insufficient lighting of milking parlours has been associated with an increased presence of the bacterium in the facilities, perhaps because this condition hinders the cleaning and disinfection process (Sanaa et al., 1993). The ability of the bacterium to produce biofilms and adhere to several surfaces constitutes another important problem, especially in animal feeders, which are susceptible to wear on a regular basis. *L. monocytogenes* has the capacity to form biofilms on plastic, rubber and stainless-steel materials, which are frequently found in milking equipment and other farm equipment (Latorre et al., 2010). Once attached, if the environment is humid, the bacterium finally finds favourable conditions for growth (Lakicevic et al., 2015). In a recent study (Ripolles-Avila et al., 2020), the efficacy of an enzymatic detergent for the detachment of *L. monocytogenes* biofilm cells from surfaces was shown; the efficiency was enhanced when the number of treatment cycles was increased. However, after this intervention, the authors highlighted the need for further disinfection, which also improved the global efficacy in the elimination of biofilms. Correct and frequent cleaning of farm surfaces, especially during winter months when the animals are crowded, is an essential practice to reduce bacterial multiplication in the stable environment.

6. Milking and raw-milk contamination

Milk is especially susceptible to bacterial proliferation, and contamination during and after milking is frequent. Poor herd hygiene and poor milking hygiene can facilitate the transmission of the bacterium from the environment to the milk bulk tank. The presence of *L. monocytogenes* in milk has been associated with its presence in faecal samples and is directly correlated with animal housing during cold months (Husu, 1990) and with poor quality of silage (Sanaa et al., 1993). It has been shown that *L. monocytogenes* is more prevalent in faecal samples than in milk samples (Table 3), highlighting the importance of these animals as active reservoirs of the bacterium (Mohammed et al., 2019).

L. monocytogenes has been detected in milk bulk tanks (Table 4) and in milk-vending machines, with a prevalence of 0.5% and at levels <10 cfu ml^{-1} (Dalzini et al., 2016). Even though the prevalence and pathogen concentration are low, the presence of the bacterium represents an important risk for human foodborne infection, especially when unpasteurized dairy products are consumed (Osman et al., 2014).

Faecal contamination is the most common route of milk bulk tank contamination. Many factors can contribute to the bacteria reaching raw milk at this stage. Practices of pre-milking teat disinfection or the use of

Table 3
Presence of *L. monocytogenes* in dairy farms: prevalence in animal faeces and raw milk.

Animal	Geographical localization	Number of Farms/herds tested	Type of production	Period	Prevalence in animal faeces	Prevalence in milk	References
Cattle	Central New York State	50	Milking cows	2003–2006	43% (608/1414)	13% (184/1412)	Mohammed et al. (2009)
	Central and southern California	25	Cow-calf and feedlot operations	3 times a year	0.3%–3.7%	*nd*	Mohammed et al. (2010)
	Mainly New York State	52	Mainly dairy cattle farms	2001–2003	62.5% 7.5%	*nd*	Nightingale et al. (2005)
	Ireland	4	Farms supplying milk to the unpasteurized milk cheese industry	3 consecutive months	12% (4/34)	0%	Fox et al.,2009
	Italy	942	Cow milk	2019–2013	*nd*	1.7% (145/8716) (2.2%	Dalzini et al. (2016)
	Finland	3	Milking cows	2013–2016	23% (39/169)	13% (25/186)	Castro et al. (2018)
	France	128	Dairy farms	1989	*Not studied*	3%	Sanaa et al. (1993)
	Tennessee	4	Dairy farms	2002–2003	1.2% (1/86)	0% (0/49)	Murinda et al. (2004)
Small ruminants	Austria	53	Ovine and caprine farms with raw milk processed to cheese and sold directly to consumers	2009	13%	0%	Schoder et al. (2011)
	Egypt	*Nd*	Dairy farms sheep and goat	*nd*	*nd*	1.4%	Osman et al. (2014)
Ruminants	Australia	7	Dairy farms	2013–2014	6% (1/16)	0% (0/15)	MacDade and Hall, 1964

Nd: not studied, not applicable or not indicated data.

Table 4
L. monocytogenes detection in udders, bulk tank milk and other milking equipment.

Listeria monocytogenes in milking operations (ruminants)						
Type of sample	Animal	Type of production	Geographical localization	Number of farms tested	Prevalence	References
Udders	Cattle	Milking cows	Central New York State	50	19% (268/1408)	Mohammed et al. (2009)
			Finland	3	17.3% (14/81)	Castro et al. (2018)
Udder wipes used					13.3% (6/45)	
In line milk filters			Central New York State	50	45% (62/137)	Mohammed et al. (2009)
			Italy	27	0.5% (2/378)	Giacometti et al. (2012)
		Dairy farm	Tennessee	4	4.1% (1/24)	Murinda et al., 2004
	Ruminants		Australia	7	11% (1/9)	MacDade and Hall, 1964
	Small ruminants	Ovine and caprine milking farms	Austria	53	2.7%	Schoder et al. (2011)
Milk filter tube	Cattle	Milking cows	Finland	3	4.3% (4/92)	Castro et al. (2018)
Milk collector					0.9% (1/91)	
Milk sample cup					6.7% (2/30)	
Bulk milk samples	Cattle		Central New York State	50	16% (22/137)	Mohammed et al. (2009)
	Cattle		Italy	942	2.2% (131/5897)	Dalzini et al., 2016
Bulk milk tank outlet	Cattle		Finland	3	2.7% (2/74)	Castro et al. (2018)
Teat cups rack					4.1% (2/48)	
Stall mats					3.3% (2/61)	
Working bench and other equipment	Small ruminants	Ovine and caprine milking farms	Austria	53	4.7%	Schoder et al. (2011)

pipeline systems rather than bulk milk systems have been associated with a low risk of *L. monocytogenes* detection (Constable et al., 2016). Specific *L. monocytogenes* strains have been associated with the colonization of milk lines, possibly due to their great ability to form biofilms in this environment for growth (Kostakioti et al., 2013; Latorre et al., 2011), which makes eradication of the bacterium from milk equipment difficult (Oliver et al., 2005). It has also been suggested that contaminated milk in bulk tanks can also act as a source of contamination for the rest of the milking system. (Castro et al., 2018). Therefore, once the bacterium has reached the milk bulk tank, it is recommended to use pre-cooling systems to maintain low bacterial counts (Paludetti et al., 2018).

Dirty udders have been described as an important source of milk contamination (Castro et al., 2018), with a prevalence of up to 19% (Mohammed et al., 2019) (Table 4). The bacterium has been reported to be present the surface of uninfected udders or inside the udders, with the latter occurring when there is an infection, such as mastitis. Milk contamination has been associated with incorrect udder hygiene or towel disinfection between milking (Sanaa et al., 1993). Previous studies have shown how incorrect disinfection of udder wipes and towels is associated with contamination of raw milk with *L. monocytogenes* (Sanaa et al., 1993). Castro et al. (2018) found a contamination prevalence on

udder surfaces and on udder wipes used after milking of 17.3% and 13.3%. To avoid contamination at this stage, a strict hygiene protocol must be followed at each milking, with continuous health and hygiene monitoring of animals. In particular, mastitis control routines during each milking are necessary, as well as pre-milking sanitation procedures, which include teat disinfection. The perimammary area of the sheep must be shorn, and bedding must be in good condition to avoid bacterial contamination. Farmers must utilize single-use udder wipes or individual cotton towels that must be disinfected after each milking. Milking should be performed in a hygienic manner, avoiding air inlets and falling teat cups. These practices help not only to reduce microbial contamination before the milking procedure but also to decrease the incidence of udder infections and clinical listeriosis (Hassan et al., 2001; Nightingale et al., 2005).

Milking filters are another important indicator of milk contamination. Poor milking hygiene increases the proportion of debris on the filter surface, which favours the attachment of *L. monocytogenes*. A milk filter that tested positive for the bacterium is a clear indicator of the presence of the pathogen in the herd and the failure of pre-harvest practices and milking hygiene. It has been suggested that the milk filters are a more sensitive indicator of the bacteria entering the bulk tank than the milk samples alone (Giacometti et al., 2012). Therefore, the screening of filters can be a good method for detecting sanitation problems, not only at the milking level but also in the environment of the herd (Castro et al., 2018). To avoid contamination at this stage of production, correct maintenance is recommended, which includes frequent cleaning, disinfection and changing of these filters to improve the likelihood of detecting bacterial contamination.

Other factors that contribute to the contamination of raw milk at milking are generally poor hygiene, including the hygienic status of the work benches, milk collectors, stall mats, teat cup racks, milk cups and other parts of the milking system that favour bacterial attachment. Good hygiene plans and correct lighting of the facilities during milking operations are necessary to minimize the risk of contamination. It is also recommended that, for good maintenance, the installations should have smooth milk contact surfaces with minimal joints and crevices and that the rubber components should be replaced at regular intervals (Sanaa et al., 1993).

7. Conclusions

In this review, we have summarized the different sources of *L. monocytogenes* contamination described in production farms, and we have analysed the available control measures to reduce bacterial levels and the risk of infection. Feedstuffs are important sources of contamination, and poor-quality silages are primarily responsible for animal carriage and listeriosis outbreaks. Long-term storage and rapid pH acidification (lower than 4.5) can inhibit the multiplication and survival of the bacterium. Although pastures can be contaminated by faecal shedding of wild and farm animals, the exposure to *L. monocytogenes* is less than that observed when the animals are housed. Furthermore, access to pasture is an important and beneficial practice not only in terms of listeriosis but also for the physical health, welfare and handling of animals. Regarding wild animals, the access of birds, mice or rats to stocked cereals and grains intended for the herd may cause further contamination. The faeces or carcasses of these animals can contaminate feed, feed bunkers, water and other surfaces on farms. Birds or vermin can cause damage (holes) in silages, leading to marked oxygen penetration and bacterial multiplication. Water and farm soils have also been described as sources of bacterial contamination. Establishing protection zones along surface watercourses, within farms and in buffer zones around farms has been shown to be effective in reducing contamination, as well as maintaining cleanliness of water troughs, pipes, taps and tanks, especially during winter months, when animals are crowded. Proper disinfection of soils is an important practice to reduce the spread of bacteria, especially with the use of enzymatic detergent to detach *L. monocytogenes* biofilm cells from surfaces. Correct management and storage of manure and control of foreign agents, with special attention to vehicle wheels, visitor boots and other materials brought into the farm, are necessary to maintain the global hygiene of the farm. Our analysis reveals the impact of bedding materials and quality on *L. monocytogenes* persistence, transmission and udder contamination. Good quality and assessment of the dryness of the material used for bedding are important measures to minimize contamination. Furthermore, investigation of the different materials for bedding replenishment revealed differences in bacterial counts and altered frequencies. Several studies on manure pathogens have provided a large number of measures to minimize contamination in farms, pastures and crops. It is necessary to avoid the application of fresh animal manure on land, and instead, it is recommended that manure treatment methods, such as pasteurization, anaerobic digestion in biodigesters, chemical disinfection, biogas production and aeration, be introduced. The storage systems of manure must be batch operated, and the storage facilities should be covered to prevent runoff in the environment and block access for wild animals. We also highlight the impact of good hygiene during milking to prevent raw milk contamination, including frequent cleaning and elimination of biofilms from all the equipment. However, in this review analysis, we clearly show that good hygiene practices are not the only important factor in this last part of production, as most of the contamination comes from animal and environmental management. Therefore, all the measures established in the farm and its surroundings at each stage of production will have an important impact on the presence and final counts of *L. monocytogenes* in raw milk.

Funding

This work was not supported by any external funding.

Ethical statement

Ethical statement is not applicable.

Data sharing statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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