REVIEW
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Microbial adaptation mechanisms in chicken meat processing and their presence in serovars of salmonellosis cases in Brazil: an integrative review

Mecanismos de adaptação microbiana no processamento da carne de frango e sua presença em sorovares de casos de salmonelose no Brasil: revisão integrativa

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ABSTRACT

Introduction: Brazil is the world's largest exporter of chicken meat. Poultry and poultry products are often associated with non-typhoidal *Salmonella* (NTS) contamination. Reports on antimicrobial-resistant (AMR) NTS serovars in isolates from Brazilian poultry farms and products are concerning. In response, interventions are implemented in poultry chains to remove microbial contaminants, but they may also exert selective bacterial pressure. **Objective:** To characterize the adaptation mechanisms occurring in *Salmonella* throughout chicken meat processing and to determine whether these mechanisms are present in antimicrobial-resistant serovars commonly reported in avian-associated salmonellosis cases in Brazil. **Methods:** This is an integrative literature review conducted in the PubMed, Embase, Scopus, SciELO, and Web of Science databases. A total of 823 studies were selected between 2017 and 2023. **Results:** Currently, the primary serovars of NTS isolated from Brazilian poultry products are S. Minnesota and Heidelberg. Antimicrobial resistance genes and multidrug resistance were detected in both serovars. However, there are no official data on cases of antimicrobial-resistant infections in humans caused by S. Minnesota and Heidelberg in Brazil, which complicates the assessment of the impact of these serovars on the country's public health. **Conclusions:** The presence of NTS and the substitution of serovars over the past decade have been observed throughout the Brazilian poultry production chain. However, there are no official data identifying the serovars and antimicrobial resistance in cases of salmonellosis in Brazil. This review suggested that this information is crucial for understanding the adaptation of these serovars in poultry processing facilities and for the development of effective strategies to control and prevent the emergence of AMR.

KEYWORDS: Non-typhoidal *Salmonella*; Salmonellosis; Cross-contamination; Antimicrobial Resistance; Chicken

RESUMO

Introdução: O Brasil é o maior exportador de carne de frango do mundo. Aves e produtos avícolas são frequentemente associados à contaminação por *Salmonella* não-tifoide (SNT). Relatos de sorovares de SNT resistentes a antimicrobianos (RAM) em isolados de granjas e produtos avícolas brasileiros são preocupantes. Diante disso, intervenções são implementadas na cadeia avícola para remover contaminantes microbianos, porém podem também exercer uma pressão seletiva bacteriana. **Objetivo:** Caracterizar os mecanismos de adaptações que ocorrem *Salmonella* ao longo do processamento de carne de frango e relacionar se estão presentes em sorovares RAM comumente relatados em casos de salmonelose associados a aves no Brasil. **Método:** Trata-se de uma revisão integrativa da literatura realizada nas bases de dados PubMed, Embase, Scopus, SciELO e *Web of Science*. Selecionou-se 823 estudos entre 2017 e 2023. **Resultados:** Na atualidade, os

principais sorovares de SNT isolados de produtos avícolas brasileiros são S. Minnesota e S. Heidelberg. Em ambos foram detectados genes de resistência antimicrobiana e multirresistência. Porém, não há dados oficiais sobre casos de infecções com RAM em humanos causadas por S. Minnesota e S. Heidelberg no Brasil, o que dificulta a avaliação do impacto desses sorotipos na saúde pública do país. **Conclusões:** A presença de SNT e sua substituição por novos sorovares, na última década, foi observada em toda a cadeia produtiva avícola brasileira. Entretanto, não existem dados oficiais que identifiquem os sorotipos e a RAM nos casos de salmonelose no Brasil. Esta revisão sugere que esta informação é crucial para compreender a adaptação desses sorovares em instalações de processamento de aves e para o desenvolvimento de estratégias eficazes para controlar e prevenir o surgimento de resistência antimicrobiana.

PALAVRAS-CHAVE: *Salmonella* não-tifoide; Salmonelose; Contaminação Cruzada; Resistência Antimicrobina; Frango

INTRODUCTION

Antibiotics are considered one of the most important advances in modern medicine due to their ability to treat and prevent bacterial infections[1]. However, their overuse in humans and animals leads to antimicrobial resistance (AMR)[2]. AMR-carrying bacteria, such as *Salmonella* spp., may be present in farm animals and transmitted to humans through the consumption of contaminated food or direct contact with these animals and their environment[3,4,5,6]. Animal products contaminated with *Salmonella* account for 3% of foodborne bacterial diseases caused by worldwide, infecting approximately 90 million people and killing 155,000 each year[6].

Salmonella enterica is one of two species of the genus Salmonella, which are rod-shaped Gram-negative bacilli belonging to the family *Enterobacteriaceae*. *S. enterica* is divided into six subspecies, including *S. enterica subsp. enterica*[7], which includes serotypes responsible for infectious diseases in humans. These diseases are classified as enteric fever (or typhoid fever), caused by S. *Typhi* and S. *Paratyphi* A, B, and C, which affect only humans, and nontyphoidal salmonellosis, caused by other serotypes that can infect both humans and animals[8]. Nontyphoidal Salmonella (NTS) generally causes mild to moderate gastroenteritis, characterized by vomiting, nausea, diarrhea, and abdominal pain[9]. Typically, these symptoms are resolved within two to seven days because they are self-limiting and do not require treatment[10]. However, the infection can progress to a more severe disease called invasive non-typhoidal salmonellosis, which can cause bacteremia, meningitis, and other focal infections[11]. The genetic variability of NTS favors its survival and spread across a wide variety of environments and hosts[12]. In fact, it is widely distributed throughout the poultry production chain, which serves as an important reservoir for transmission to humans[13]. NTS isolates with AMR have frequently been identified on farms, in slaughterhouses, meat processing facilities, and clinical trials in various countries[14,15].

Brazil is the world's second-largest producer of chicken meat and the largest exporter of chicken meat, exporting more than 4 million tons of chicken annually to over 150 countries[16]. It is essential that chicken products are safe to prevent the global spread of AMR-carrying SNT serotypes. In Brazil, measures to reduce and restrict the use of antimicrobials in animals have been implemented. Since the ban on the use of various antimicrobial compounds due to regulations from the Ministry of Agriculture, Livestock, and Supply, the use of antimicrobials as performance-enhancing additives has been declining[17].

However, chicken meat processing involves steps that expose carcasses to heat, cold, and osmotic pressure (washing), which reduce, modify, and select the microbiota of the final product[18]. And this exposure to stress can also induce adaptive changes in the *Salmonella* transcriptome and proteome[19]. *Salmonella* isolates in poultry products or processing plants may also be antimicrobial-tolerant, even without ever having been exposed to antibiotics during production [20].

Based on these aspects, the present integrative review addressed the possible routes of contamination and the adaptive changes in *Salmonella* throughout the main stages of chicken meat processing. Furthermore, we sought to understand whether these changes are present in serovars with a higher prevalence of AMR commonly reported in cases of salmonellosis associated with poultry in Brazil.

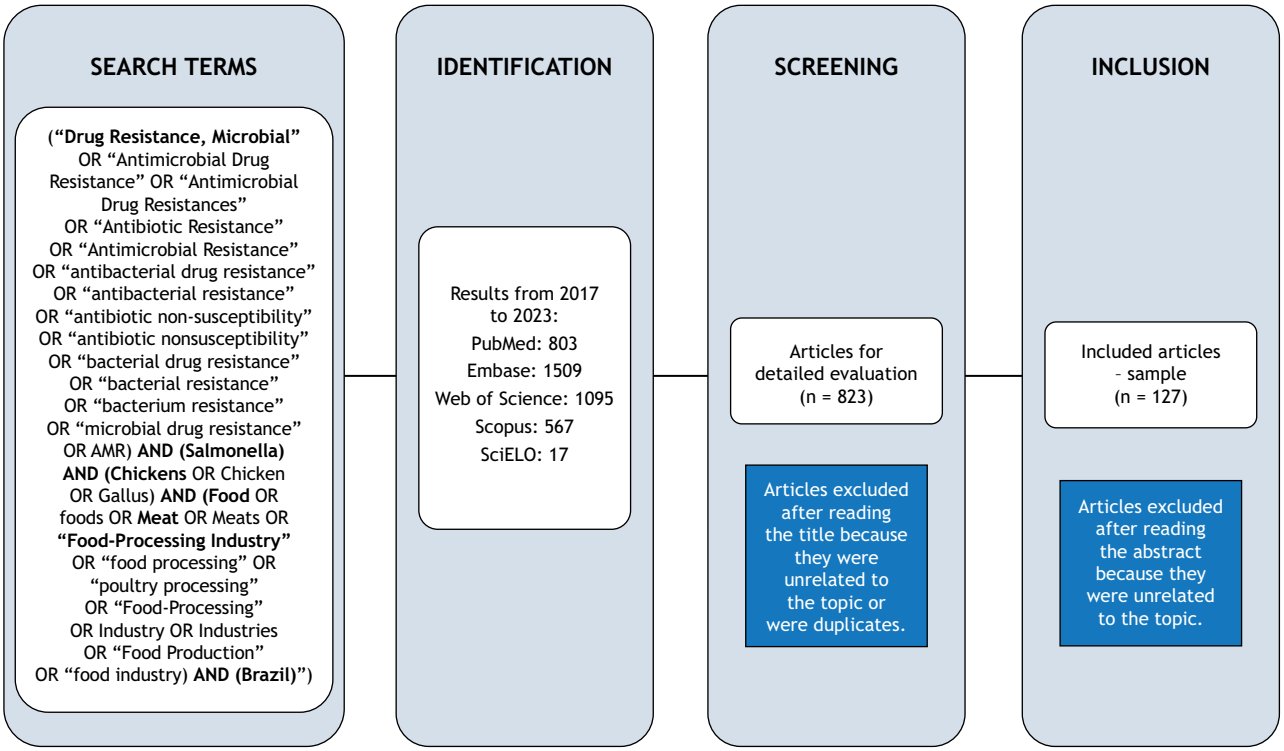
METHOD

According to Souza et al.[21], an integrative literature review is a resource that enables the synthesis and critical analysis of research on a specific topic. This method provides evidence-based guidance. This review covered the period from January 2017 to April 2023. The databases consulted were U.S. National Library of Medicine (PubMed), Biomedical Literature Database (Embase), Expertly Curated Abstract & Citation Database (Scopus), Scientific Electronic Library Online (SciELO), and Web of Science. Study selection was based on search terms, and inclusion criteria considered the relevance of the title and abstract to the proposed topic. The selected publications were retrieved in full text to assess their eligibility, and duplicates were excluded. Figure 1 shows the article selection criteria for the integrative review.

RESULTS AND DISCUSSION

Stages of chicken meat processing that favor *Salmonella* contamination

Poultry meat production is carried out intensively at high densities across a range of operations, including breeder



Source: Prepared by the authors, 2023.

Figure 1. Flowchart of the article selection process for the integrative review.

farms, hatcher farms, broiler farms, and slaughter and carcass processing facilities[22]. Contamination with SNT serotypes can occur at any of these production stages. *Salmonella* can contaminate the broiler production chain through contaminated feed, rodents, wild birds, or other biosecurity breaches[23,24,25].

However, contamination of broiler chickens with *Salmonella* generally occurs through horizontal transmission from the environment via feed, water, insects (flies), and microorganisms (amoebae, yeasts, and molds)[26] and through the indirect horizontal method of spread via chicken litter on farms[27]. Once *Salmonella* enters a flock, it spreads rapidly, colonizing the gut (feces, small intestine, and cecum), the skin, and the feathers of most animals within a week [28]. Birds infected with SNT serovars can contaminate processing facilities through transport crates, equipment, surfaces, utensils, employees, water, air, and dust[29,30].

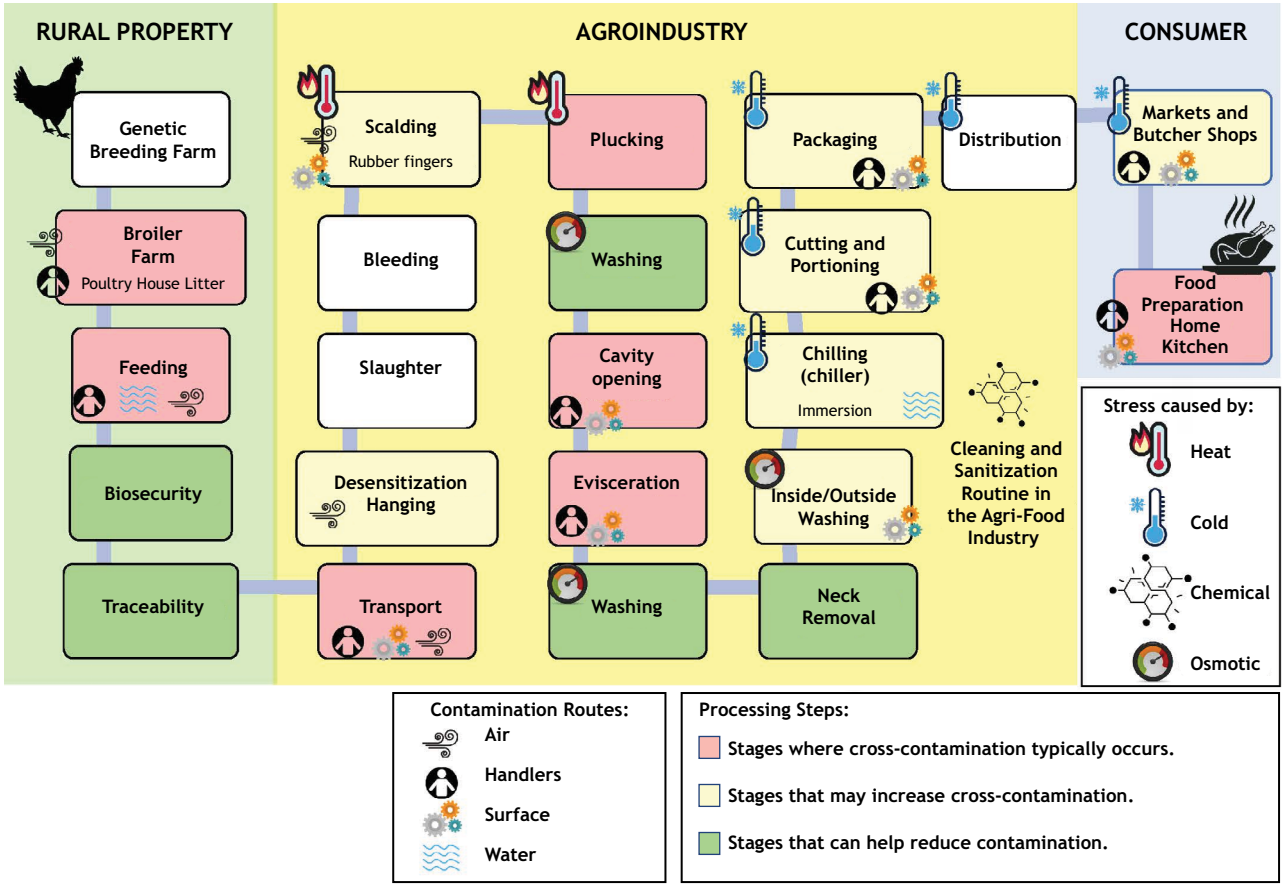
Salmonella can also spread through vertical transmission, via contamination of the egg in the reproductive tract of breeding birds before shell formation, or penetration of the microorganism through the shell after laying[31], though this is uncommon in breeding birds.

Procedures such as feed withdrawal prior to transport can also spread *Salmonella*. Nutrient limitation can result in a less diverse and competitive microbiota, subsequently increasing the growth of pathogenic bacteria[32]. Feed withdrawal is a commercial practice in which producers remove feed from the birds in poultry houses, usually 8 to 10 hours before transport, to reduce the amount of feces in the gastrointestinal tract of broiler chickens. Thus, a reduced probability of fecal contamination during automated evisceration is assumed[33,34].

Regarding transport conditions, overcrowding of chickens in cages and the stress induced by this stage may increase the shedding of *Salmonella* in feces. When the chickens arrive at the slaughterhouse, they may be kept in an antechamber to calm down before slaughter. During this period, the birds may lie down, increasing body contact with feces; therefore, proper cleaning and disinfection of the conveyor belts and crates are important measures to minimize the possibility of cross-contamination and subsequent spread of bacteria[35].

In processing, after stunning and slaughter, plucking is performed in stages: scalding and plucking, a method that can contribute to cross-contamination of microorganisms such as *Salmonella* from the feathers to the birds' skin[36,37]. However, other studies have reported the opposite[38,39,40]. The type of equipment used for scalding and the temperature can be decisive factors in the occurrence of cross-contamination at this stage. Figure 2 illustrates the main common steps in poultry processing in Brazil that can increase or decrease the likelihood of cross-contamination.

The scalding step is important for loosening the feathers from the carcasses before the plucking process. It can be performed



Source: Prepared by the authors, 2023.

Figure 2. Schematic diagram showing the main stages of the chicken slaughtering process and possible sources of contamination.

using two distinct systems: immersion scalding in hot water baths, ranging from a few seconds to 2 minutes, and spray scalding. During immersion scalding, bacteria can be removed by the washing effect and high temperature. However, studies have shown the occurrence of cross-contamination at this stage due to the accumulation of dirt in the tank[36,41,42].

In immersion scalding, the introduction of fecal matter causes the water's pH to decrease due to the dissociation of ammonium urate, present in chicken feces, into uric acid and ammonium hydroxide, which increases heat resistance for *Salmonella*[43]. During steam scalding, bacteria are reduced solely by the effect of temperature, and cross-contamination appears to be lower because the carcasses are not immersed in water [44].

Scalding conditions may vary depending on the chicken processing method (chilled or frozen), as this step can affect meat characteristics such as the skin color of fresh chicken [45]. In the U.S., heavy scalding (water temperature: 60–66°C and immersion time of 45 to 90 seconds) is the commonly used procedure, while in Europe, light scalding (water temperature: 51–54°C and immersion time of 120 to 210 seconds) is more widely used[46]. In Brazil, the scalding temperature in meatpacking plants is around 55°C[47].

The plucking process, which completely removes the feathers from the chicken carcass, is also a critical step, as the pressure exerted by the equipment (sets of motorized discs with rubber fingers) often causes fecal leakage[48]. Studies have shown that the surface of the rubber fingers is a source of bacterial contamination within the slaughterhouse[29,49,50].

During the scalding and plucking stages, heating the skin can increase its permeability, also causing cross-contamination with the industrial environment. Heating the skin opens the skin follicles to remove the feathers; the empty follicular cavity acquires negative pressure, which can draw fluid from the skin's surface, allowing the penetration of microorganisms and dirt particles. In view of this, microbial contamination in poultry occurs mainly on the skin, as it has a large surface area and comes into contact with various sources of contamination[51].

Furthermore, chicken skin has a high lipid content and features microfolds, follicles, and microcracks, creating microenvironments that provide protection from processing stresses to bacteria such as *Salmonella*[51,52].

The next step in processing is evisceration, the goal of which is to completely remove the intestinal tract without causing rupture.

The entire evisceration process is automated, so it is a major challenge to properly eviscerate (without causing fecal leakage or gastrointestinal rupture) chicken carcasses of varying sizes due to the heterogeneity of the carcasses. Since conventional equipment cannot be individually adjusted for each carcass, only batch adjustments are permitted, so accidental cutting of other intestinal sections may occur, causing fecal leakage and contaminating the carcasses[34].

During the cooling stage, the carcass may be subjected to immersion in a counter-current cold-water tank (chiller), air cooling, or spray cooling (the carcasses are sprayed with water at various points in the cooling room). The purpose of the chiller is to reduce the carcass temperature to below 7°C[47], prevent the growth of pathogens and control the overall microbial load, as well as increase shelf life and improve sensory characteristics[53].

Some meat processing plants use these combined immersion and air-cooling systems, with a cold-water tank at the beginning of the process. The cooling method used depends on the scalding temperature regime. When scalding temperatures are very high, cooling must be by immersion, as the skin is removed and the carcasses must be kept moist during the process; otherwise, the appearance of the chicken skin/meat is affected [34].

Immersion cooling is more effective in reducing the microbial load due to the washing effect[54,55,56]. However, the immersion method can contribute to cross-contamination between carcasses[56,57,58]. Immersion cooling is the predominant practice in the United States, the world's largest producer, and in Brazil, the world's largest exporter of chicken, while air cooling is the most widely used technology in Europe[56,59].

The effective implementation of strategies to control SNT in integrated poultry companies is, therefore, difficult. Serotypes, as well as genotypes, must be considered to understand the dynamics of this pathogen in these production systems[25].

All these processing stages may cause changes in the microbial cell of *Salmonella*.

Bacterial adaptation for survival during chicken meat processing

Studies suggest that *Salmonella* isolates can persist despite sanitation steps at various points in the production chain[25]. The survival rate of microorganisms during exposure to different processing conditions will depend on the initial level of contamination in the chicken carcasses received from the farm and the effects of antimicrobial intervention strategies applied during processing and handling[60].

Salmonella possesses different signal transduction systems that allow it to detect environmental stimuli, such as sudden changes in pH, osmolarity, temperature, toxic compounds, and many others, by modulating the expression of specific genes[61]. These systems alter individual cells and colonies, as responses such as biofilm formation are induced to promote bacterial survival[62].

One of the most widely studied signal transduction systems used by bacteria is the two-component regulatory system (TCS). It consists of a membrane protein that detects the external stimulus and a cytoplasmic regulatory protein that modulates the expression of specific target genes that are somehow related to the stimulus[61]. *Salmonella's* two-component regulatory system is a complex web of interactions among systems that monitor the environment and regulate motility, metabolism, anaerobic respiration, resistance to antimicrobial compounds, and virulence. Exposure of *Salmonella* to processing stresses can trigger TCS, as well as dormancy. This strategy allows *Salmonella* to enter a viable but non-cultivable state when exposed to stressful environmental changes, remaining non-growing but still alive. When conditions become favorable again, these cells return to a normal metabolic state[61,63,64,65].

The main decontamination treatments commonly used in commercial plants are: thermal, washing (osmotic/pressure), and chemical.

Thermal treatment

Thermal interventions involving the use of high or low temperatures have been used for several years to control pathogenic bacteria. *Salmonella* has an optimal multiplication temperature of 37°C, with some strains capable of surviving at extremely low or high temperatures (2°C to 54°C)[66].

To tolerate thermal stress, the first cellular response is the expression of genes related to stress and energy metabolism[65]. However, this can lead to cross-resistance to various other types of stress, thereby increasing its virulence potential, whether through the expression of fimbriae, increased adhesion capacity, or survival within the host[67,68].

Heat shock

Scalding water temperatures (≈ 56°C) cause severe thermal damage to bacterial cell structures, leading to protein misfolding, enzyme denaturation, and cell membrane disruption[19]. Heat damages cells by denaturing proteins, destroying cellular structures, and disrupting metabolic processes. These effects occur more rapidly than cellular repair mechanisms can respond[19,69,70,71]. According to Dawoud et al.[72], the survival of *Salmonella* during heat treatment can be explained by several factors. One of them is that heat penetration is not uniform, making it unable to eradicate all contamination[65,73,74].

Therefore, during scalding, *Salmonella* attached to the skin is able to tolerate and adapt[57]. Another reason is that *Salmonella's* survival capacity is increased when pre-exposed to stressful conditions before the carcass is heat-treated. Cells stressed by heat, low-carbon sources, desiccation, or starvation tend to have greater tolerance to heat treatments[65]. Bacterial adaptation to stressful environments occurs via thermal sensors, which are cellular structures that detect internal temperature fluctuations and induce adaptive and protective gene expression[75,76]. Alternative sigma factors control bacterial gene expression by detecting changes in the environment[77]. The Sigma factor σ^E protects the cell against stress fluctuations and regulates extracellular responses, while σ^H regulates the

cytoplasmic response to thermal stress through the transcription of heat shock genes. RpoS is another example, acting primarily on protein expression and the regulation of virulence genes[78,79,80]. Heat treatment of *Salmonella* can also stimulate the expression of virulence genes[81].

Yang et al.[82] reported that transcription of *rpoH* genes in *Salmonella* Enteritidis reached its highest level when cultured at 42°C. Furthermore, all virulence genes were upregulated in response to high temperature. The mechanism involved is the activation and specific transcription of *rpoH* genes under high temperature[77,82,83].

Cold shock

Cooling is an important antimicrobial barrier introduced during processing; however, it can drive the development and selection of phenotypic variants that may respond with physical changes induced by low temperature[84]. Low temperatures also slow microbial multiplication by reducing membrane fluidity, stabilizing RNA structure, and reducing the overall efficiency of transcription, translation, and degradation processes, in addition to reducing nutrient uptake [85,86,87].

The production of proteins (Hsp70, GroEL, DnaK, GrpE, etc.) during cold shock allows the bacterium to better survive under stressful conditions, even participating in adhesion and invasion processes[88,89]. There is an acclimation phase in which protective measures increase cellular resilience to low temperatures. *Salmonella* spp. uses cold shock proteins (CSPs) as a response for rapid adaptation to reductions in ambient temperature[65]. CSPs are produced during the acclimation phase (temperature reduction) from 30°C to 10°C[77]. Studies have been conducted on *Salmonella's* ability to increase its survival rate by expressing a CSP when treated at low temperatures (5°C to 10°C) prior to freezing[90,91,92]. *Salmonella* Enteritidis was able to survive in chicken parts at 2°C, while *S.* Typhimurium survived in ground meat at 2°C; *S.* Panama also showed a high propensity to survive on agar at 4°C, and *S.* Typhimurium and *S.* Tennessee were able to survive in environments below 10°C[77,92,93]. *S.* Typhimurium undergoes cold-induced upregulation of genes necessary for adhesion and invasion of Caco-2 epithelial cells, while the virulence-related SPI-1 and SPI-2 T3SS show upregulation in response to cold exposure due to cold shock protein activity and the activity of SpvR and SpvABC[93]. These serovars can survive prolonged exposure to cold and enter the food chain through contaminated meat products.

Once acclimated, the cells resume a normal growth pattern and have a reduced need for CSPs and stress response proteins[93,94]. Shah et al.[95] demonstrated that when *S. Typhimurium* was pre-acclimated to cold stress, it was tolerant to subsequent acid stress.

Chemical treatment

In some countries, such as China and the United States, low concentrations of chemicals—including chlorine derivatives, trisodium phosphate, and organic acids—are used during carcass washing[96,97,98]. Brazilian legislation does not permit the addition of chemicals during carcass washing; only potable water with a maximum chlorine content of 5 ppm is allowed[47]. However, the use of chemicals as sanitizers is permitted for production line facilities, equipment, utensils, and transport crates. This is part of the routine operational procedures for poultry processing. The main sanitizers in the poultry industry are triclosan, quaternary ammonium compounds, hypochlorite salts, peracetic acid, chlorhexidine, and ethanol[99,100]. Modern sanitizing compounds use low-pH components or oxidizing compounds to exert acid, oxidative, and chemical stress on bacterial cells[20].

However, some microorganisms, such as *Salmonella*, can adhere to the surfaces of food processing equipment, forming biofilms that remain active after cleaning and sanitization[101,102,103]. These biofilms can protect bacteria from sanitizers through the extracellular matrix[24], while cell clustering can facilitate the transfer of AMR genes via horizontal gene transfer[104]. Furthermore, biofilm efflux systems enable bacterial persistence on routinely cleaned surfaces, such as meat cutting boards, increasing the community's tolerance to severe sanitizing stresses[20].

In particular, hyperactive efflux pumps and alterations in the outer membrane have been proposed as broad-spectrum mechanisms conferring tolerance and/or resistance to antimicrobials in *Salmonella* following exposure to hexadecylpyridinium chloride and trisodium phosphate[105,106]. This allows *Salmonella* to survive, contaminating chicken meat on affected contact surfaces, potentially leading to cross-contamination of a *Salmonella*-free batch during processing[107,108].

Acid stress can activate RpoS, a central sigma factor in *Salmonella*, and its induction confers cross-resistance under various subsequent stresses, including cold and heat stress as previously observed[19,109,110]. However, its role in modulating cellular expression patterns in response to stress extends to affect more cellular functions. This increases *Salmonella's* resilience in the processing environment, including by altering cellular metabolism and the virulence of the species. Studies have shown that acidic pH significantly affects *Salmonella* gene expression[61,111,112]. Ryan et al.[111] conducted a transcriptome analysis of bacteria cultured under conditions that activated the acid tolerance response and found that a large number of genes (47% of the genome) were differentially expressed (change of 1.5-fold or more).

Resistance-nodulation-division (RND) pump systems are commonly employed for the efflux of unwanted molecules, including disinfectants and antibiotics, from the cellular cytosol, such as AcrAB-TolC, found in *Salmonella*. AcrAB-TolC, an archetypal RND efflux system, is induced in conjunction with a reduction in cell permeability in response to the detection of antimicrobial compounds. This increases resilience to chemical stress along with bacterial tolerance to common industrial cleaning procedures[113]. Triclosan, a sanitizer

used in food industry settings, is expelled from *Salmonella* biofilms via AcrAB-TolC systems, thereby compromising its efficacy[98,114].

It has been demonstrated that repeated exposure and subinhibitory concentrations of sanitizers allow bacteria to adapt, resulting in antibiotic-resistant and sanitizer-tolerant bacteria[20,115]. The potency of sanitizing agents is essential for the inactivation of *Salmonella* during the sanitization procedure. Effective concentrations of sanitizers must be tested on biofilms and sessile planktonic cells[20].

The Multiple Antibiotic Resistance (*marAB*) operon is a global regulator of AMR genes, including the *acrAB* and *tolC* genes. Its expression is increased in biofilm-associated *Salmonella* cells through the relief of MarR repression of *marAB*, leading to increased efflux via MarA[19]. Under normal conditions, expression of the *Salmonella* efflux system is repressed by the TetR-type transcriptional repressor, which controls the overexpression of *acrAB*. However, exogenous stress leads to relief of TetR repression[116,117,118]. This occurs in response to chemical signals, including phenols, antimicrobial compounds, and reactive oxidative species (ROS)[19].

Osmotic shock

The abundance of ions, biomolecules, and cellular components within the cell cytoplasm creates a hyperosmotic environment in which biological reactions and processes can occur [119,120]. Osmotic stress is a predominant part of processing; Hypoosmotic environments, such as washing steps, can cause uncontrolled water influx into the cell, leading to increased intracellular pressure. This can reduce the efficiency of processes such as transcription, which requires cellular proximate components [19].

Further swelling puts the cell at risk of lysis due to high internal pressure within the cell, especially if the cell wall is compromised[120,121]. The hyperosmotic conditions that occur during air drying and cooling lead to cellular shrinkage as water leaves the cell, causing cell crowding and turgor (the force exerted by stored water against a cell wall) to decrease to physiologically unsustainable levels[119,120]. Since water moves freely across the cell membrane, a bacterial cell must respond rapidly to combat stress and adapt to function as effectively as possible. Initial responses to osmotic stress include the rapid import/export of small, charged solutes, such as potassium cations, via transporters that increase/decrease cytoplasmic osmolarity[119]. Hypoosmotic stress leads to the opening of the mechanosensitive channels MscS and MscL in the cell membrane due to increased internal pressure and cell conductance. These channels relieve internal pressure on the cell membrane, reducing the likelihood of lysis[120,121]. Extended bacterial survival requires the synthesis and accumulation and/or import/export of organic solutes such as: proline, glycine betaine, proline betaine, carnitine, ectoine, trehalose, dimethylsulfoniopropionate, hydroxyectoine, and glucosylglyceroll[120]. These solutes are preferable by the cell over time, as they do not affect cellular function through altered protein folding in the same way that charged solutes, such as metal cations [119].

Major *Salmonella* serovars in Brazilian chicken meat and cases of salmonellosis associated with chickens in Brazil

In Brazil, the most concerning serovars in poultry production throughout the 20th century were the same as those in other Western chicken-producing countries: Gallinarum, Typhimurium, and Enteritidis. Currently, a decrease in *Salmonella* Enteritidis has been observed, followed by an increase in the *Salmonella* Minnesota and *Salmonella* Heidelberg serovars in poultry after 2003, the year the Enteritidis vaccine was introduced. The prevalence of S. Heidelberg ranged from 40.0% to 87.0%[122,123] and the rates of S. Minnesota ranged from 11.6%[122] to 88.0%[124], making them the most common serovars in the Brazilian poultry industry[17].

Morasi et al.[125] analyzed 238 isolates from chicken breast samples collected over two decades (1999–2010 and 2011–2018) in the Southeast Region. In the first decade, the most frequent serotypes were S. Enteritidis (42.3%, 58/137) and S. Ohio (28.3%, 36/137), while S. Heidelberg (25.7%, 26/101) and S. Typhimurium (21.8%, 22/101) were the most prevalent in the second decade, confirming the replacement of new serotypes in the chicken supply chain. In addition, they observed a significant increase in the number of multidrug-resistant *Salmonella* spp. isolates and extended-spectrum beta-lactamase (ESBL)-producing strains that hydrolyze cephalosporins in poultry meat over the two-decade period, which is likely a result of the selection of resistant bacteria.

The higher frequency of S. Heidelberg in the last decade was also observed in the study by Gomes et al.[126], in which 386 samples of chicken parts (wing, breast, thigh, and drumstick) were analyzed, yielding a frequency of 72.4% of isolates as S. Heidelberg, with 79.3% exhibiting multidrug resistance. In the two studies by Morasi et al.[125] and Gomes et al.[126], the samples were obtained from butcher shops and retail outlets and not directly from the production line. However, Gomes et al.[126] found that, although contamination was slightly higher in small butcher shops, samples from supermarkets and hypermarkets also tested positive, a finding worthy of note. The resistance profiles and genotypes observed indicate that meat contamination originates in production systems or meat-processing plants and does not suggest cross-contamination in the markets evaluated.

Dias et al.[17] analyzed 97 non-typhoid *Salmonella enterica* non-typhoid from broiler chickens (n = 34) and carcasses (n = 63) from the Midwest, South, and Southeast regions of Brazil recovered in 2013, 2017, 2018, 2019, and 2020 from the chicken meat processing line. The results showed a high prevalence (85.6%) of *Salmonella* spp. in samples collected over the seven-year period in Brazil, with S. Heidelberg being the most common serotype.

Salmonella Heidelberg is the most commonly isolated serovar in Brazilian poultry farming and has been associated with a diverse repertoire of antimicrobial resistance genes and mobile genetic elements[122,123,127]. These mobile genetic elements may contain multiple antimicrobial resistance genes that can be easily transferred to other strains, and co-select resistant strains, even in the absence of antibiotic exposure[1,127]. The prevalence of ciprofloxacin-nonsusceptible *Salmonella* in poultry and poultry products from Brazil ranged from 56.8% (83/146) in 2014 to 89.0% (145/163) in 2017[122]. The high frequency of resistance detected by Rau et al.[122] in 2017 was similar to current results, which suggested that resistance to ciprofloxacin in *Salmonella* spp. and serovars isolated from the poultry industry is, for the most part, dose dependent

Since poultry and poultry products are considered one of the main sources of human infection, this represents a serious threat to public health[17]. People infected with *Salmonella* may be asymptomatic or develop enteric disease, which can include bloody diarrhea, fever, headache, nausea, abdominal pain, and vomiting, and in some cases, trigger severe systemic illness[128]. Salmonellosis does not require antibiotic treatment, but in patients with immunosuppression, persistent diarrhea, or invasive infection, treatment with antibiotics, such as ciprofloxacin, is necessary. Studies in Brazil and other countries involving *Salmonella* spp. isolated from humans have shown a decrease in susceptibility to ciprofloxacin since 2010[129,130]. Human infection with ciprofloxacin-resistant strains has been associated with treatment failure and/or delayed response to treatment[131].

According to the Ministry of Health[132], between 2009 and 2018, *Salmonella* spp. was the second leading cause of foodborne illness in the country, accounting for 11.2% of reported outbreaks. Updated data from the Epidemiological Bulletin of the Health Surveillance Secretariat[133] showed that, between January 2016 and December 2019, the prevalence of *Salmonella* spp. outbreaks increased by 14.9%. Voss-Rech et al.[134] and Mendonça et al.[135] identified *S.* Typhimurium, *S.* Enteritidis, *S.* Infantis, *S.* Heidelberg, *S.* Newport, *S.* Hadar, *S.* Mbandaka, and *S.* Senftenberg as the most common serovars in Brazil.

Fernandes et al.[136] analyzed 3,553 clinical isolates from hospitals in São Paulo between 2004 and 2020 and found a prevalence of 41.9% for *S.* Enteritidis (1,489); 11.4% for *S.* Typhimurium (406), and only 0.3% for the *S.* Heidelberg serovar (12). According to Fernandes et al.[136], when comparing the frequencies of the main serotypes over the analyzed periods, they observed a strong and significant decline for *S.* Enteritidis, while other serovars showed consistent growth in their frequencies. Studies by Mascitti et al.[137] and Reis et al.[138] also reached this conclusion. Mascitti et al.[137] analyzed 789 clinical isolates from 2000 to 2019 in the Southeast Region, finding a prevalence of *S.* Enteritidis (359, 45.50%) and *S.* Typhimurium (79, 10.01%) in the samples. Reis et al.[138] analyzed 307 clinical isolates from the Central Laboratory of the State of Rio Grande do Sul (LACEN-RS) collected from cases of salmonellosis in hospitalized patients or ongoing emerging cases in the Southern Region of Brazil from 2010 to 2015. They found a higher prevalence of *S.* Typhimurium (48.4%, 140 isolates) and *S.* Enteritidis (18.3%, 53 isolates). Globally, *S.* Enteritidis and *S.* Typhimurium are also the two most important SNT serovars transmitted from animals to humans[139].

As global chicken consumption continues to grow, a corresponding increase in the risk associated with the spread of antibiotic-resistant bacteria is observed. Therefore, it is imperative to consider the potential risk of allowing the introduction of new serovars into the chicken supply chain that exhibit conditional adaptation and/or antibiotic resistance [140].

According to Alikhan et al.[141], the *S.* Heidelberg and Minnesota serovars have shown a weaker association with clinical disease in animals and a low incidence of disease in humans. Following the identification of these serovars in broiler chickens in Brazil—including those exported to countries such as the United Kingdom—they were analyzed. The occurrence of human infections related to these serovars remains low, including in the United Kingdom[17]. However, it is important to note that the characteristics of AMR element mobilization associated with these serotypes have the potential to spread widely, both biologically and geographically.

CONCLUSIONS

Salmonella serovars are resilient microorganisms with complex genomic systems that allow them to respond to various adverse environmental conditions on the farm, during processing, and in facilities. Based on this brief review, we can identify critical production stages where SNT can enter the broiler chicken production chain. Stages such as scalding, plucking, and evisceration can increase the likelihood of cross-contamination on the processing line[57].

Therefore, despite the establishment of bacterial control barriers, *Salmonella* contamination can adapt to stress and induce a wide variety of adaptive mechanisms, such as the production of stress proteins, biofilm formation, and virulence. Phenotypic and genotypic changes can occur in individual bacterial cells or in biofilms, allowing *Salmonella* to withstand extreme stress, which may influence the phenotypes of bacteria entering.

The presence of SNT and its replacement by new serovars over time have been observed throughout the Brazilian poultry production chain. A decrease in the frequency of *S.* Enteritidis and an increase in the *S.* Minnesota and *S.* Heidelberg serovars are observed in poultry and meat with RAM. Unfortunately, there are no official data on human infections by *S.* Minnesota and Heidelberg in Brazil to assess whether or not these serovars have an impact on Brazilian public health. Thus, they pose a health threat and a risk to the poultry market.

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Authors' Contributions

Laranja DC - Conception, planning (study design), data collection, analysis, interpretation, and writing of the manuscript. Geimba MP - Conception, planning (study design), and writing of the manuscript. All authors approved the final version of the manuscript.

Conflict of Interest

The authors declare that there is no potential conflict of interest with peers, institutions, politicians, or financial entities related to this study.

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