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# Comparative genomic analysis of *Salmonella* Enteritidis from Kazakhstan in a regional context

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## Abstract

*Salmonella enterica* causes salmonellosis, posing a threat to food safety and public health. Wild and domestic birds serve as major natural reservoirs of *Salmonella*. Furthermore, antimicrobial use in livestock production has been recognized as a key factor contributing to the emergence of antimicrobial resistance in nontyphoidal *Salmonella*. In Kazakhstan, poultry accounts for 83% of total meat imports, with Russia and China remaining the country's major trading partners. Enteritidis is the most prevalent *Salmonella* serovar in Kazakhstan. However, genomic data on *S.* Enteritidis isolates circulating in Kazakhstan remain fragmented and do not adequately characterize the population structure of this serovar.

Publicly available whole-genome sequencing (WGS) data from *S.* Enteritidis isolates collected in Kazakhstan (n = 15) were analyzed and compared with those from neighboring countries sharing land borders and maintaining extensive trade relations with Kazakhstan: China (n = 48), Russia (n = 27), and Kyrgyzstan (n = 1). Raw sequencing reads were retrieved from the Sequence Read Archive (SRA) and assembled using Shovill (Illumina) and Flye (Oxford Nanopore). Assembly quality was assessed using QUAST, serovars were predicted using SISTR, and sequence types were determined using mlst. Core-genome alignment was performed using Parsnp, followed by the identification and removal of recombinant regions using Gubbins. A maximum-likelihood phylogenetic tree was constructed using IQ-TREE. Antimicrobial resistance genes were identified using StarAMR and AMRFinderPlus.

Four major phylogenetic clades were identified. Chinese isolates formed a distinct clade, whereas Kazakhstani isolates were distributed across three clades together with Russian isolates rather than forming a single phylogenetic group. Antimicrobial resistance genes were detected in 80 of 91 genomes (87.9%), with 36 of 91 (39.6%) exhibiting multidrug resistance (MDR)-associated genetic determinants. The most frequently detected resistance gene was $bla_{TEM}$, followed by mutations in *gyrA* associated with quinolone resistance.

The analyzed *S.* Enteritidis isolates from Kazakhstan exhibited genetic heterogeneity and varying degrees of genetic relatedness to Russian isolates. Mutations associated with fluoroquinolone resistance were detected in approximately one-third of the Kazakhstani isolates, raising concerns about the effectiveness of this class of antibiotics for treatment. These findings highlight the need for systematic genomic surveillance of *S.* Enteritidis in Kazakhstan.

**Keywords: *Salmonella* Enteritidis; Kazakhstan; genomic epidemiology; phylogeny; antimicrobial resistance**

# Introduction

Food security has become a major research priority across various scientific disciplines in the context of global economic and climate change. Salmonellosis is one of the major zoonotic infections posing a threat to food safety. *Salmonella* is a genus of Gram-negative, rod-shaped bacteria comprising two species, *Salmonella enterica* and *Salmonella bongori*. Of particular epidemiological importance is the subspecies *S. enterica* subsp. *enterica*, which encompasses more than 1,500 serovars.

Kazakhstan is among the countries with a relatively low reported incidence of salmonellosis (Table 1). A decline in the number of reported cases was observed in 2020–2021, potentially reflecting the impact of quarantine measures implemented in response to the SARS-CoV-2 pandemic [1]. In 2023, a total of 944 salmonellosis cases were reported nationwide, including 136 cases associated with outbreaks. Among *Salmonella* isolates recovered from patients, serovar Enteritidis predominated, accounting for 86.9% of cases [2].

**Table 1.** Incidence of salmonellosis in the population of the Republic of Kazakhstan, 2019–2024 [3].

| No. of cases | 2019 | 2020 | 2021 | 2022 | 2023 | 2024 |
|---|---|---|---|---|---|---|
| Total number of cases (thousands) | 1.1 | 0.5 | 0.5 | 0.9 | 0.9 | 0.9 |
| Cases per 100,000 population | 5.9 | 2.7 | 2.6 | 4.6 | 4.7 | 4.8 |

Official surveillance statistics may not fully reflect the true burden of salmonellosis. A substantial proportion of infections are mild, do not require medical attention, and consequently remain unreported. Furthermore, epidemiological surveillance in many countries is constrained by limited laboratory diagnostic capacity [4].

Salmonellosis remains a major concern in epidemiology and clinical medicine and imposes substantial economic losses on the food industry and livestock production, particularly the poultry sector. Poultry production is one of the major sectors of Kazakhstan's agricultural industry. As of June 2026, the national poultry population was approximately 49 million birds, representing a 2.6% increase compared with the corresponding period in 2025 [5]. Nevertheless, Kazakhstan remains heavily dependent on imports. In 2025, the country imported 136.7 thousand tons of poultry meat, accounting for 83% of total meat imports [6]. Russia and China are Kazakhstan's major trading partners, accounting for 43.3% and 14.9%, respectively, of total imports of meat and edible offal during January–July 2026 [7], a trade pattern largely influenced by the country's geographical location.

Poultry and eggs are major reservoirs and vehicles of transmission, respectively, for *Salmonella* Enteritidis. The use of antimicrobial agents in livestock production is recognized as an important driver of antimicrobial resistance in nontyphoidal *Salmonella*, which can be transmitted to humans through the food chain [8]. In Kazakhstan, *Salmonella* isolates, including those belonging to serovar Enteritidis, have been detected in industrial poultry production facilities, with resistance to several antimicrobial agents reported [9].

A recent large-scale longitudinal ecological and modelling study encompassing more than 480,000 *Salmonella* genomes from 139 countries over the period 1940–2023 reported a 38% increase in the global mean number of antimicrobial resistance genes per cell, with further increases projected [10].

The population structure of *Salmonella enterica* in Kazakhstan remains poorly characterized. Publicly available genomic sequences of Kazakhstani isolates have been deposited as part of individual studies that differ in their isolate selection criteria, sampling sources, and completeness of associated metadata [11, 12]. Consequently, genomic data on nontyphoidal *Salmonella* circulating in Kazakhstan remain limited and fragmented. Whole-genome sequencing (WGS) provides an opportunity to address this knowledge gap by generating a broad range of epidemiologically relevant information within a single analytical framework [13].

However, none of these studies has examined the regional context. As a result, the phylogenetic structure of *S.* Enteritidis in Kazakhstan and the genetic relatedness of Kazakhstani isolates to those from neighboring countries remain insufficiently characterized.

The present study aimed to characterize the phylogenetic relationships and antimicrobial resistance profiles of all publicly available *Salmonella* Enteritidis genomes from Kazakhstan through comparative genomic analysis with isolates from neighboring countries that share land borders with Kazakhstan and represent its major trading partners.

# Materials and Methods

## Study Design

A retrospective comparative genomic analysis was conducted using publicly available *S.* Enteritidis genome sequences. The dataset included isolates originating from Kazakhstan and neighboring countries sharing a land border with Kazakhstan. Isolates were compared based on their phylogenetic relationships and antimicrobial resistance gene profiles.

## Data Collection

The analysis was designed to include genomes from countries sharing a land border with Kazakhstan (the Russian Federation, the People's Republic of China, the Kyrgyz Republic, the Republic of Uzbekistan, and Turkmenistan). However, publicly available *S.* Enteritidis genomes were identified only for Russia, China, and Kyrgyzstan.

Given the substantial differences in the amount of publicly available genomic data among countries, Chinese genomes were selected using a stratified sampling approach. All available *S.* Enteritidis genome sequences from the Xinjiang Uyghur Autonomous Region, which borders Kazakhstan, were included. For the remaining Chinese provinces, sampling was restricted to poultry-associated isolates, with several genomes selected from each province to ensure broad geographical coverage while preventing individual regions from being overrepresented in the dataset. All available genomes from Russia and Kyrgyzstan were included because of their limited numbers.

The final dataset comprised isolates originating from Kazakhstan (n = 15), China (n = 48), Russia (n = 27), and Kyrgyzstan (n = 1) (Fig. 1).




**Figure 1.** Geographic origin of the analyzed *S.* Enteritidis genomes; circles indicate sampling locations, colored by country.

Sequencing reads were retrieved from the SRA database using the SRA Toolkit. Illumina reads were assembled with Shovill v1.4.2 [14] with read trimming enabled and an expected genome size of 4.8 Mb; Oxford Nanopore reads were assembled with Flye v2.9.6-b1802 [15] using the same expected genome size. Assembly quality was assessed with QUAST v5.3.0 [16]. Assemblies were retained only if total length was 4.0–6.5 Mb, N50 ≥ 10 kb, and the number of contigs ≥ 500 bp was below 1000. Isolate metadata and assembly quality metrics are provided in S1 Table.

## Bioinformatics Analysis

Serovars were predicted based on cgMLST using SISTR v1.1.3 [17]. Sequence types were determined with mlst v2.35.0 [18] (*Salmonella enterica* scheme) based on the PubMLST database [19]. Antimicrobial resistance genes were identified with StarAMR v0.12.3 [20] (ResFinder and PointFinder databases, organism *Salmonella*) and AMRFinderPlus v4.2.7 [21] DB version 2026-05-15.1 (organism *Salmonella*); virulence genes were identified with ABRicate v1.4.0 [22] (VFDB database [23]). Isolates carrying acquired genes or chromosomal point mutations associated with resistance to ≥3 antimicrobial classes were classified as having a multidrug-resistant (MDR) genotype, adapting Magiorakos et al. [24]. Sulfonamide and trimethoprim determinants were counted as one class (folate pathway inhibitors). Resistance markers for quaternary ammonium compounds, bleomycin, lincosamides, streptothricin and tylosin are listed in S1 Table but excluded from the count, as these agents are not used to treat *Enterobacterales* infections.

Core-genome alignment against the reference strain *S.* Enteritidis P125109 (GCA_000009505.1) was performed with Parsnp v2.1.5 [25], and recombinant regions were removed with Gubbins v3.4.3 [26]. A maximum-likelihood phylogenetic tree was inferred with IQ-TREE v3.1.2 [27] under the GTR+ASC model; branch support was assessed by ultrafast bootstrap [28] and SH-aLRT (1,000 replicates each). Pairwise genetic distances were calculated from the recombination-filtered polymorphic site alignment using snp-dists v0.8.2 [29]. NCBI Pathogen Detection data were used to assess the genetic relatedness inferred from the phylogenetic analysis. The phylogenetic tree was visualized using iTOL [30]. Isolate RU01 was used as an outgroup to root the phylogenetic tree and was subsequently omitted from the

visualization to improve the clarity of the tree topology and branch length scale. Statistical analyses and data visualization were performed using R version 4.5.2 [31] using the ggplot2 package v4.0.3 [32]. Scripts and input tables are available at github.com/alinamustafina02-netizen/salmonella-enteritidis-genomic-epidemiology.

# Results

## Phylogenetic analysis of S. Enteritidis isolates

In this study, whole-genome sequencing data from Kazakhstani *S.* Enteritidis isolates were used for comparative genomic analysis. We hypothesized that Kazakhstani isolates would exhibit phylogenetic relatedness to isolates from neighboring countries that share land borders with Kazakhstan and maintain established trade relationships involving poultry and poultry products.

Clades were defined as monophyletic groups with ultrafast bootstrap support ≥ 95%. Four major clades (C1–C4) were identified in the phylogenetic tree (Fig. 2).

The reference genome was removed from the phylogenetic tree visualization after tree construction. Isolate RU01 from the Russian Federation did not belong to any of the four identified clades and exhibited an average pairwise genetic distance of 1,866 SNPs from the remaining isolates.

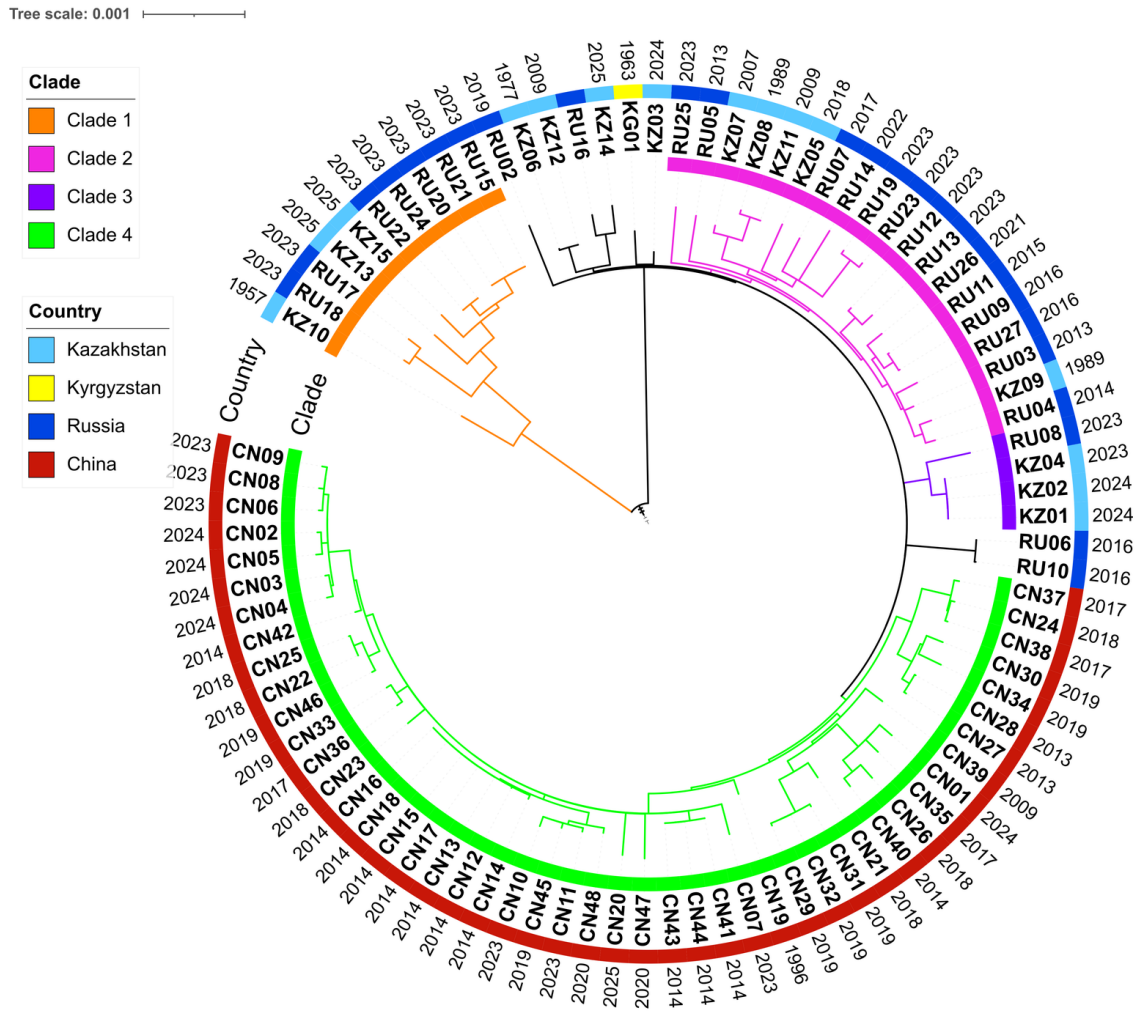


**Figure 2.** Maximum likelihood tree of 91 *S.* Enteritidis genomes; node circles indicate ultrafast bootstrap support ≥95%, the inner strip shows clades C1–C4, the outer strip the country of origin, and the numbers indicate the year of isolation.

In the resulting phylogenetic tree, Kazakhstani isolates did not form a single distinct cluster but were distributed across three clades together with Russian isolates. Chinese isolates formed a separate clade, designated C4.

Isolates KZ03, KZ06, KZ12, and KZ14 did not belong to any of the four identified clades. According to NCBI Pathogen Detection [33], KZ06 and KZ12 belonged to SNP cluster PDS000274801.1, which was comprised of Kazakhstani isolates. Isolate KZ14 belonged to SNP cluster PDS000084711.702, with its closest related isolates originating from the United States and the United Kingdom. SNP cluster PDS000271162.22, which included isolate KZ03, exhibited broad geographical diversity, comprising genomes from Europe, Africa, and Russia.

MLST analysis identified isolates RU01, RU18, and RU23 as single-locus variants (SLVs) of ST11, corresponding to ST136, ST10712, and ST10717, respectively. All remaining genomes were assigned to ST11.

Pairwise SNP distances varied considerably among isolates from different countries. Chinese isolates exhibited relatively low genetic diversity, with a mean pairwise distance of 58 SNPs and a maximum of 111 SNPs. In contrast, maximum pairwise distances among Russian isolates (excluding RU01) and Kazakhstani isolates reached 486 and 466 SNPs, respectively. For 12 of the 15 Kazakhstani isolates, the closest genome originated from Russia, whereas for the remaining three, the closest genome originated from China, with SNP distances to the nearest Chinese genomes being only 3–4 SNPs smaller than those to the nearest Russian genomes. The minimum intercountry genetic distance was 18 SNPs, observed between isolates KZ09 and RU04.

## In silico antimicrobial resistance prediction

Antimicrobial resistance genes conferring resistance to three or more classes of antibiotics were identified in 36 of 91 isolates (39.6%), indicating genotypic multidrug resistance (MDR) profiles. An important distinction is that MDR is primarily a phenotypic classification, whereas whole-genome sequencing identifies genetic determinants associated with antimicrobial resistance. Of these 36 isolates, 34 (94.4%) belonged to the Chinese clade. No genetic determinants associated with multidrug resistance were detected among the Kazakhstani isolates.

A total of 29 antimicrobial resistance genes and resistance-associated mutations were identified, representing resistance to seven classes of antimicrobial agents (Fig. 3). The greatest diversity of resistance markers was observed for quinolones (n = 9).

The virulence factor repertoire was highly conserved, with genes associated with *Salmonella* pathogenicity islands SPI-1, SPI-2, SPI-3, SPI-4, and SPI-5 detected in all isolates. The number of virulence factor (VF) genes ranged from 153 to 166 per genome.

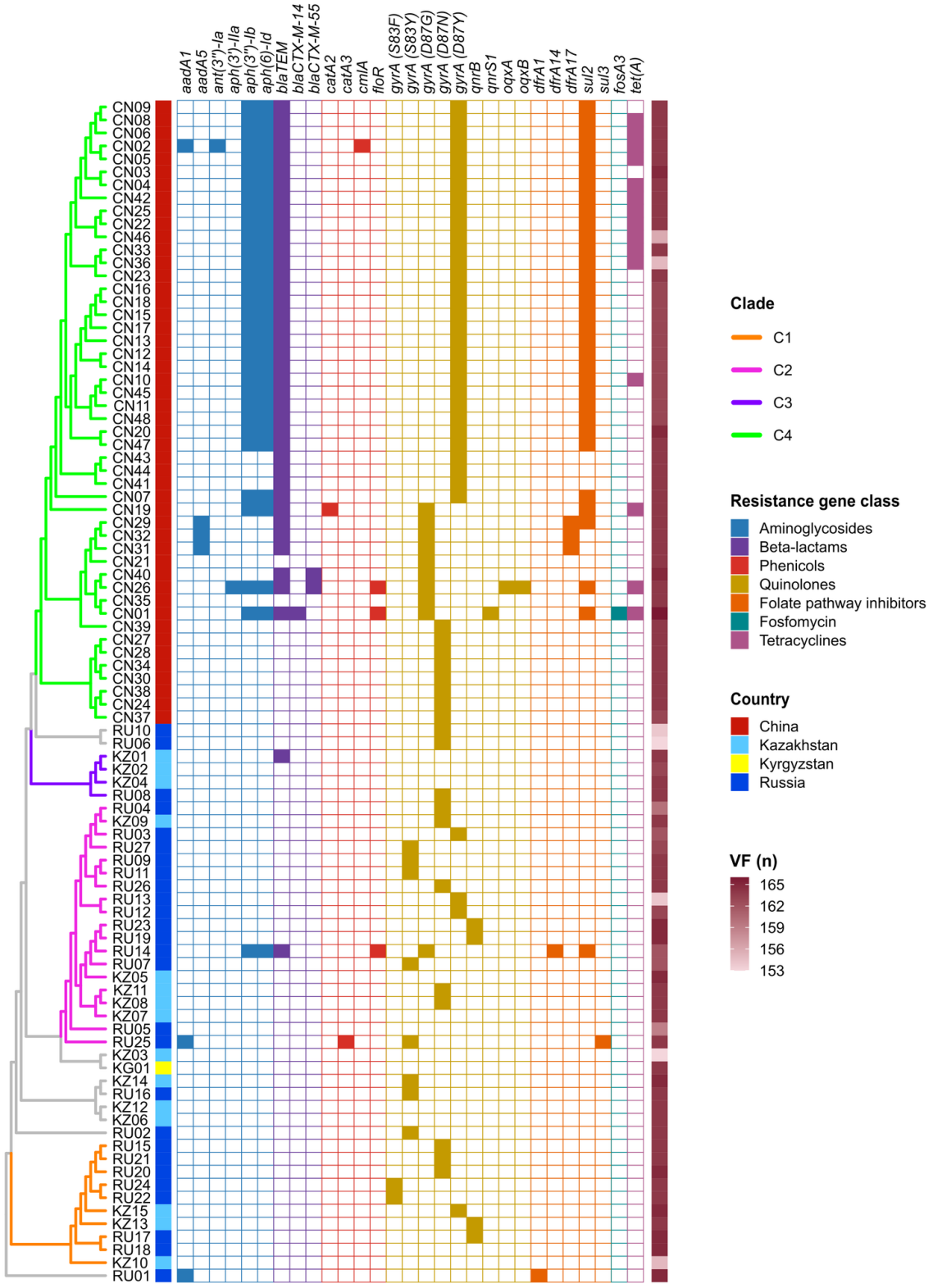



**Figure 3.** Antimicrobial resistance and virulence gene content across 91 *S.* Enteritidis genomes; rows are ordered according to the phylogeny, columns show resistance genes grouped by antimicrobial class, and VF indicates the number of virulence factor genes per genome.

The greatest diversity of antimicrobial resistance determinants was observed for quinolones, which inhibit bacterial DNA gyrase and topoisomerase IV. Nine distinct resistance markers were identified,

including five amino acid substitution variants in *gyrA*, encoding the A subunit of DNA gyrase, and four genes associated with plasmid-mediated resistance or efflux mechanisms. Mutations in *gyrA* were detected in 74 of 91 isolates. The most prevalent acquired resistance gene was *bla*$_{TEM}$ (40/91), whereas the most frequent resistance-associated mutation was *gyrA* D87Y (35/91) (Fig. 4).

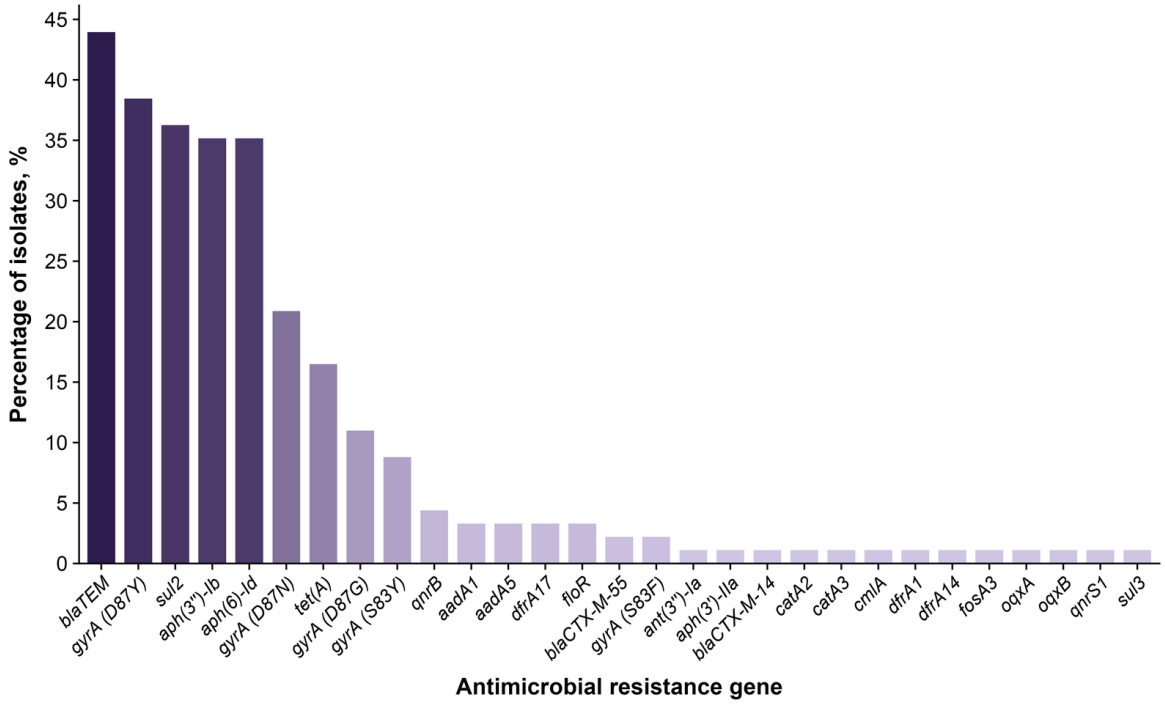



**Figure 4.** Frequency of antimicrobial resistance determinants among 91 *S.* Enteritidis genomes; color intensity is proportional to frequency.

The *bla*$_{TEM}$ gene, encoding a narrow-spectrum β-lactamase, was detected in 40 of 91 isolates. For some detections, the specific allele could not be determined because the identified sequences covered only a portion of the gene. Genes encoding extended-spectrum β-lactamases (ESBLs) were detected in a small number of isolates: *bla*$_{CTX-M-14}$ (1/91) and *bla*$_{CTX-M-55}$ (2/91). Two of the three isolates carrying ESBL genes also harbored resistance determinants associated with quinolones and aminoglycosides, consistent with previous reports [34].

In 15 of 91 isolates (16.5%) belonging to clade C4 (Fig. 2), characteristic combinations of antimicrobial resistance genes, including *sul2*, *aph(3")-Ib*, *aph(6)-Id*, *bla*$_{TEM}$, and *tet*(A), were identified. These combinations are consistent with resistance gene profiles reported in *S. enterica* isolates circulating in China [35].

## Discussion

The main limitation of the phylogenetic analysis was the lack of a representative dataset due to the limited availability of genomic data from Kazakhstani isolates in public databases. Consequently, the present study does not provide a comprehensive characterization of the population structure of *S.* Enteritidis in Kazakhstan. The available Kazakhstani genomes span the period from 1957 to 2025, with nearly half originating from before 2010, whereas the Chinese and Russian isolates were predominantly collected in more recent years. Furthermore, most publicly available Kazakhstani genomes were not derived from poultry or poultry products; therefore, the contribution of poultry production to the dissemination of antimicrobial-resistant isolates in Kazakhstan could not be assessed in this study.

Reliable reconstruction of the transmission pathways of *S.* Enteritidis requires systematic accumulation of genomic data and their integration with epidemiological surveillance findings.

Nevertheless, the findings of this study may provide a foundation for further investigations into the population structure of *S.* Enteritidis in the region.

*Salmonella* Enteritidis exhibits a highly clonal population structure and relatively low genetic diversity. The vast majority of *S.* Enteritidis isolates worldwide belong to sequence type ST11, as demonstrated by numerous studies [36–38].

In the present study, 97% of the isolates were assigned to ST11, highlighting the limited discriminatory power of conventional multilocus sequence typing (MLST) for resolving the genetic diversity within this serovar. Therefore, phylogenetic clades were delineated based on the topology of the phylogenetic tree.

Kazakhstani isolates were distributed across three clades and exhibited genetic relatedness to Russian genomes. These findings do not support the hypothesis of a single Kazakhstan-specific phylogenetic lineage and are consistent with the possibility of multiple independent introductions of *S.* Enteritidis into Kazakhstan.

For most Kazakhstani isolates, the genetic relatedness to Russian isolates inferred from the phylogenetic analysis was also supported by NCBI Pathogen Detection data, which provide comparisons against a substantially broader collection of deposited genomes. This suggests that the observed relationships were not solely attributable to the composition of the study dataset. However, isolates KZ10, KZ13, and KZ15, which clustered with Russian genomes in the phylogenetic tree, were assigned by NCBI Pathogen Detection to SNP clusters predominantly comprising isolates from the United Kingdom and the United States. This finding highlights the geographical limitations of the study dataset, which did not include closely related isolates from other countries.

The greater genetic diversity observed among Kazakhstani and Russian isolates compared with Chinese isolates likely reflects differences in temporal coverage and sampling strategies rather than genuine differences in the population structures of *S.* Enteritidis across these countries.

Increasing antimicrobial resistance remains a major concern in both clinical medicine and livestock production. This issue is particularly relevant for serovars with highly clonal population structures, as the dissemination of resistant clones may facilitate the persistence and spread of antimicrobial resistance determinants within bacterial populations.

Quinolones and third- and fourth-generation cephalosporins are classified by the World Health Organization (WHO) among the highest-priority critically important antimicrobials (HPCIAs) [39]. These antimicrobial agents remain important treatment options for severe salmonellosis, and in some clinical circumstances, therapeutic alternatives may be limited. Therefore, the identification of genetic markers associated with resistance to these agents is of direct clinical relevance.

Kazakhstani isolates exhibited relatively few antimicrobial resistance determinants compared with isolates from China and Russia, and none displayed a genotypic multidrug resistance (MDR) profile. Nevertheless, mutations in *gyrA* associated with quinolone resistance were detected in five isolates, while the plasmid-mediated resistance gene *qnrB* was identified in one isolate. Mutations in *gyrA* represented the most frequently detected quinolone resistance mechanism in the Kazakhstani dataset. Single mutations in this gene can confer resistance to nalidixic acid and reduce susceptibility to fluoroquinolones [40, 41], potentially compromising the effectiveness of treatment for severe salmonellosis. Thus, the absence of genotypic MDR does not diminish the clinical significance of the detected resistance-associated mutations.

Quinolone resistance is widespread among poultry-associated *Salmonella* isolates [42]. However, published phenotypic antimicrobial susceptibility data for *Salmonella* isolates from poultry production facilities in Kazakhstan primarily concern aminoglycosides and tetracyclines, with no reported data on fluoroquinolone susceptibility [9]. Our findings highlight the need to include fluoroquinolones in antimicrobial resistance surveillance programs.

Antimicrobial resistance profiles differed substantially among countries. Mutations in *gyrA* predominated among Russian isolates, whereas genes associated with resistance to multiple antimicrobial classes were detected in more than 70% of Chinese isolates. Such differences are particularly relevant for serovars with highly clonal population structures, including *S.* Enteritidis, because the spread of resistant clones may contribute to the persistence of resistance determinants within bacterial populations. Nevertheless, evidence from China indicates that the introduction of national restrictions on antimicrobial use in livestock production has been accompanied by a decline in the prevalence of multidrug-resistant *Salmonella* strains in recent years [43].

Livestock production remains an important source of *Salmonella* strains resistant to quinolones and cephalosporins [44]. In Kazakhstan, prophylactic administration of antimicrobial agents to clinically healthy animals is permitted [9], potentially creating selective pressure favoring the emergence and persistence of resistant strains. Because these strains may be transmitted to humans through the food chain, antimicrobial use in livestock production, particularly in the poultry sector, requires appropriate monitoring and control [39].

## Conclusions

The analyzed Kazakhstani *S.* Enteritidis isolates did not form a single phylogenetic group and exhibited genetic relatedness to isolates originating from Russia. The identified antimicrobial resistance determinants highlight the need for monitoring and regulating antimicrobial use in both human medicine and livestock production. These findings demonstrate the potential of whole-genome sequencing for epidemiological surveillance and underscore the need to establish a comprehensive genomic database of *Salmonella enterica* isolates in Kazakhstan.

## Abbreviations

AMR, antimicrobial resistance; cgMLST, core genome multilocus sequence typing; ESBL, extended-spectrum β-lactamase; MDR, multidrug resistance; MLST, multilocus sequence typing; SNP, single nucleotide polymorphism; SPI, *Salmonella* pathogenicity island; ST, sequence type; VF, virulence factor; VFDB, Virulence Factor Database.

## Supporting Information

**S1 Table.** Characteristics of the analyzed genomes: metadata, assembly quality metrics, serotyping, MLST, antimicrobial resistance and virulence gene profiles. XLSX, download

## Use of Generative AI

During the preparation of this manuscript, the authors used ChatGPT (OpenAI, accessed in 2026) to assist with language editing, translation, and the formatting of bibliographic references. All AI-assisted output was critically reviewed, edited, and verified by the authors against the original sources. The authors take full responsibility for the content of this publication.

## Data Availability Statement

All genomes analyzed in this study are publicly available in the NCBI databases; accession numbers are listed in S1 Table. All other relevant data are within the manuscript and its Supporting Information files. Scripts and input tables are available at github.com/alinamustafina02-netizen/salmonella-enteritidis-genomic-epidemiology.

## Author Contributions

Conceptualization: P.T.; Methodology: A.M., P.T.; Software: A.M.; Validation: A.M., P.T.; Formal analysis: A.M., S.B.; Investigation: A.M.; Data curation: A.M.; Writing – original draft: A.M.; Writing – review & editing: S.B., P.T.; Visualization: A.M.; Supervision: P.T.

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## Ethics approval and consent

Not applicable. The study did not involve humans or animals.

## Competing Interests

The authors have declared that no competing interests exist.

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