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Review Article

***Staphylococcus aureus* Bovine Mastitis: Epidemiology, Antimicrobial Resistance, and Emerging Post-Antibiotic Therapy - A Review**

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Abstract

Bovine mastitis, particularly that caused by *Staphylococcus aureus*, remains a major constraint on the global dairy industry, affecting milk quality, animal welfare, and farm profitability (Halasa *et al.*, 2007; Ruegg, 2017). This review synthesizes current knowledge of *S. aureus* epidemiology and pathogenic mechanisms, including biofilm formation and immune evasion. It examines the escalating threat of antimicrobial resistance (AMR) and methicillin-resistant *S. aureus* (MRSA) in dairy herds. Advances in diagnostics — qPCR, MALDI-TOF, and CRISPR-based biosensors — are compared with conventional detection methods and herd management practices. The review then evaluates post-antibiotic therapeutic strategies, including nanotechnology-based delivery systems, bacteriophage therapy, phage-delivered CRISPR-Cas gene editing, antimicrobial peptides, vaccination, and probiotics, weighing reported efficacy against developmental stage. We conclude by identifying three priority research gaps: translation of phage- and CRISPR-based therapeutics from murine models to field trials in cattle, harmonized regional AMR surveillance, and vaccine formulations capable of cross-protecting against genetically diverse *S. aureus* strains. *S. aureus* is recognized as a highly resistant microorganism to the majority of antibiotics, including ampicillin, amoxicillin, and native penicillins; moreover, resistance is also expanding to macrolides, tetracyclines, and lincosamides.

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1. Introduction and Epidemiology

Bovine mastitis is among the most prevalent and economically damaging diseases in the global dairy industry, characterized by mammary gland inflammation following microbial invasion through the teat canal. The disease alters milk composition, reduces yield, increases veterinary costs, and frequently leads to premature culling (Halasa *et al.*, 2007; Ruegg, 2017). Occurring as either a clinical disease or a sub-clinical, often undetected, state, mastitis reduces productivity and compromises milk quality throughout a lactation (Seegers *et al.*, 2003).

More than 140 organisms have been associated with intramammary infection, spanning contagious, environmental, and, less commonly, fungal (*Candida* spp., *Aspergillus* spp.) or algal (*Prototheca zopfii*) agents that emerge under immunosuppressive conditions (Watts, 1988; Bradley, 2002; Krukowski *et al.*, 2013). Environmental pathogens such as *Escherichia coli* and *Streptococcus uberis* exploit lapses in teat hygiene and host immunity (Hogan and Smith, 2012), while contagious pathogens — chiefly *Staphylococcus aureus*, *Streptococcus agalactiae*, and *Mycoplasma bovis* — spread cow-to-cow via milking equipment and hands, posing the greater herd-level control challenge (Keefe, 1997, 2012).

2. Pathogenic Mechanisms of *Staphylococcus aureus*

S. aureus owes much of its success as a mastitis pathogen to a diverse array of virulence factors that together enable chronic intramammary infection and frequently defeat conventional antibiotic therapy (Barkema *et al.*, 2006). Adherence is typically the first step, mediated by Microbial Surface Components Recognizing Adhesive Matrix Molecules (MSCRAMMs) — notably fibronectin-binding proteins and clumping factors — which anchor the bacterium against the mechanical flushing action of milking (Foster *et al.*, 2014).

S. aureus further sustains chronic infection by evading both humoral and neutrophil-mediated clearance, in part by invading and persisting within mammary epithelial cells, where many antibiotics achieve limited intracellular penetration (Almeida *et al.*, 1996; Sears and

McCarthy, 2003). A broader account of these host–pathogen interactions and immune-evasion strategies is provided by Rainard *et al.*, (2018). In addition, *S. aureus* frequently forms biofilms — bacterial communities encased in a protective extracellular matrix regulated by genes such as *icaA* and *icaD* — that impose a state of metabolic dormancy strongly associated with toxin production reduced antibiotic penetration and treatment failure (Melchior *et al.*, 2006; Gomes *et al.*, 2016).

3. Antimicrobial Resistance and Public Health Implications

The rise of antimicrobial resistance (AMR) in mastitis pathogens adds urgency to this disease, creating overlap between veterinary treatment failure, compromised therapeutic protocols, and wider public health concerns (Tenhagen *et al.*, 2018). Penicillin resistance is the most established example: a substantial proportion of *S. aureus* isolates carry a *blaZ*-encoded β -lactamase that inactivates ampicillin, amoxicillin, and native penicillins (Oliver and Murinda, 2012).

Methicillin-resistant *S. aureus* (MRSA), mediated by altered penicillin-binding protein PBP2a following acquisition of *mecA* or *mecC*, compounds this problem. Although its prevalence in dairy cattle is comparatively low, MRSA carries recognized zoonotic potential for farm workers and veterinarians through direct contact (Vanderhaeghen *et al.*, 2010; Kadlec *et al.*, 2010). Resistance is also expanding toward macrolides, tetracyclines, and lincosamides, and multidrug-resistant (MDR) *S. aureus* strains are increasingly reported (Jamali *et al.*, 2018; Klibi *et al.*, 2018). The dairy production chain has also been implicated as a route for plasmid-mediated AMR transmission relevant to One Health surveillance (Wang *et al.*, 2022).

4. Advancements in Diagnostics

Because a large share of *S. aureus* infections is subclinical, diagnostic precision is central to control. Somatic cell counts (SCC exceeding 200,000 cells/mL) remain a useful, low-cost, herd-level inflammatory marker. Still, pathogen-specific confirmation increasingly relies on quantitative PCR (qPCR), which targets *S. aureus*-specific markers (*spa*, *nuc*, *coa*) along-

side AMR determinants (*mecA*, *blaZ*) to inform same-day treatment decisions (**Klibi *et al.*, 2018**). MALDI-TOF (Matrix-Assisted Laser Desorption/Ionization Time-of-Flight) mass spectrometry provides rapid, accurate species identification once an isolate is in hand, and is

increasingly paired with cow-side biosensors, LAMP-based nucleic acid amplification, and CRISPR-Cas12a/Cas13a biosensor platforms capable of same-visit, field-deployable pathogen and AMR-gene detection (**Middleton *et al.*, 2014**).

Table (1). Advantages and disadvantages of each assay:

Method	Target	Turnaround	Key advantage	Key limitation
Somatic cell count (SCC)	Host inflammatory response	Minutes (cow-side)	Cheap, rapid, herd-level screening	Not pathogen-specific; threshold effects vary by parity/stage
Bacteriological culture	Viable organism, phenotype	24–72 h	Gold standard; enables susceptibility testing	Slow; intracellular/dormant cells under-detected
qPCR (<i>spa</i>, <i>nuc</i>, <i>coa</i>, <i>mecA</i>, <i>blaZ</i>)	Pathogen and AMR gene DNA	Hours (same-day)	High sensitivity; detects non-culturable/intracellular forms	Detects DNA, not necessarily viable/active infection; cost
MALDI-TOF MS	Protein mass-spectral fingerprint	Minutes post-isolation	Rapid, accurate species ID once isolate obtained	Requires prior culture; capital equipment cost
CRISPR-Cas12a/13a biosensors	Pathogen nucleic acid	< 1 h	Field-deployable, high specificity, MRSA discrimination	Early-stage validation; limited on-farm field data

5. Prevention and Herd Management Strategies

Prevention rests on integrated, herd-level hygiene and management practices rather than any single intervention (**Ruegg, 2017; Barkema *et al.*, 2009**). Core measures include post-milking teat disinfection with iodine- or chlorhexidine-based dips (**Dufour *et al.*, 2011**), selective dry-cow therapy to reduce reservoir carriage (**Halasa *et al.*, 2009**), and culling or segregation of chronically infected animals, combined with routine PCR-based milk screening (**Rinaldi *et al.*, 2022**). Nutritional immune support — notably supplementation with Vitamin E and selenium — has also been associated with reduced prevalence (**Sordillo, 2018; Oliver *et al.*, 2011**). **Barkema *et al.*, (2009)** note that the success of herd-level *S. aureus* control programs depends heavily on consistent implementation of these measures in combination, rather than on any single practice in isolation.

6. Future Frontiers: Post-Antibiotic Strategies

The strategies below are frequently grouped as "next-generation" mastitis therapeutics, but they differ substantially in their stage of development, from early in vitro proof-of-concept to field-validated, licensed products. Table 2 summarizes their mechanism and evidentiary status; the following subsections discuss each in turn, including their current limitations.

6.1. Nanotechnology-based delivery

Lipid- and chitosan-based nanoparticle carriers have been explored to improve antimicrobial penetration of the mammary gland and to disrupt established biofilms, potentially restoring efficacy to antibiotics that otherwise fail against sequestered or intracellular *S. aureus* (**Gomes and Henriques, 2023**). Evidence to date is largely in vitro or early in vivo, and translation to field-ready intramammary formulations remains an open question.

6.2. Bacteriophage therapy

Lytic bacteriophages offer a biological alternative to antibiotics, targeting *S. aureus* while sparing much of the commensal microbiota. A field trial in lactating dairy cattle found that a five-day course of intramammary phage K infusion normalized somatic cell counts in treated quarters within two weeks, although, as with extended antibiotic courses against established infections, microbiological cure of long-standing intramammary infection was not consistently achieved (Gill *et al.*, 2006). Murine mastitis models using bovine-associated phage cocktails have shown significant reductions in bacterial load and inflammation (Breyne *et al.*, 2017), and phage-cocktail approaches continue to show promise against multidrug-resistant strains (Dias *et al.*, 2024). A key open question for field application is the reduced efficacy of some phages against established, biofilm-embedded infections relative to newly acquired ones.

6.3. CRISPR-Cas and phage-delivered gene editing

CRISPR-Cas systems are being developed for both diagnosis and therapy. On the diagnostic side, Cas12a/Cas13a-based biosensors coupled to isothermal amplification can detect *S. aureus* nucleic acids, including from milk, within an hour and can discriminate MRSA from other common mastitis-associated organisms (Middleton *et al.*, 2014). On the therapeutic side, a 2026 study engineered non-replicating, phage-derived chromosomal islands (ePICIs) to deliver CRISPR-Cas9 modules targeting essential *S. aureus* small regulatory RNA genes; in a murine mastitis model, this approach achieved bactericidal activity comparable to vancomycin against biofilm-producing strains, despite the biofilm matrix conferring protection in vitro (Garmendia-Antoñana *et al.*, 2026). This is presently the most direct in vivo evidence for phage-delivered CRISPR-Cas efficacy in a mastitis model, though the authors themselves caution that the murine mammary gland is structurally simpler than the bovine udder, and that efficacy in cattle remains to be established.

6.4. Antimicrobial peptides and quorum-sensing interceptors

Synthetic antimicrobial peptides (AMPs) and inhibitors of the *agr* quorum-sensing system, which *S. aureus* uses to coordinate biofilm formation and toxin production, are under active investigation as adjuncts or alternatives to antibiotics (Li *et al.*, 2023; Pérez *et al.*, 2023). Most published data remain in vitro or early preclinical, with the cost of synthesis and in vivo stability as recognized translational barriers.

6.5. Vaccines and immunoprophylaxis

Two whole-cell bacterin vaccines are currently licensed for *S. aureus* mastitis control — Lysigin and Startvac — but field evidence of their efficacy is mixed rather than uniformly positive. A controlled heifer challenge trial found that Lysigin-vaccinated animals had a shorter duration and lower severity of clinical mastitis than unvaccinated controls, but no significant difference in intramammary infection clearance rate, somatic cell count, or milk yield (Middleton *et al.*, 2006). Leitner *et al.*, (2011) similarly report that commercial vaccine efficacy varies considerably across trials and challenge conditions, a pattern generally attributed to strain diversity and the difficulty of eliciting cross-protective immunity against a pathogen with such a broad virulence-factor repertoire. Because of this variability, vaccination is best regarded as a component of an integrated control program rather than a stand-alone solution. Newer recombinant-antigen and mRNA vaccine platforms aim to improve cross-strain protection but remain in earlier stages of development (Sharma *et al.*, 2024).

6.6. Probiotics and competitive exclusion

Lactic acid bacteria with demonstrated in vitro inhibitory activity against *S. aureus* have been proposed as a competitive-exclusion strategy within the udder or milking environment (Fernández *et al.*, 2023). As with several other strategies in this section, evidence for in vivo efficacy under commercial dairy conditions is still limited.

Table (2). Post-antibiotic therapeutic strategies against *S. aureus* mastitis, by mechanism and developmental stage.

Approach	Mechanism	Developmental stage	Representative evidence
Nanoparticle-delivered antimicrobials	Lipid/chitosan carriers improve mammary penetration and biofilm disruption.	In vitro / early in vivo	Gomes & Henriques, (2023)
Bacteriophage therapy	Lytic phages target <i>S. aureus</i> ; phage cocktails improve host-range coverage	Field trial (lactating cattle) and murine models	Gill <i>et al.</i>, 2006; Breyne <i>et al.</i>, (2017); Dias <i>et al.</i>, (2024)
Phage-delivered CRISPR-Cas9 (ePICI)	Non-replicating chromosomal islands deliver Cas9/gRNA that cleaves essential <i>S. aureus</i> sequences.	Murine mastitis model; bactericidal activity comparable to vancomycin	Garmendia-Antoñana <i>et al.</i>, (2026)
Synthetic antimicrobial peptides / agr quorum-sensing interceptors	Direct bactericidal action or disruption of virulence/biofilm signalling	In vitro / preclinical	Li <i>et al.</i>, (2023); Pérez <i>et al.</i>, (2023)
Whole-cell bacterin vaccines (Lysigin, Startvac)	Opsonising antibody response against <i>S. aureus</i> surface antigens	Licensed; field-validated with conflicting efficacy	Middleton <i>et al.</i>, (2006); Leitner <i>et al.</i>, (2011)
Recombinant/mRNA vaccines	Targeted antigen or nucleic-acid-encoded immunogen for cross-strain protection	Preclinical/early development	Sharma <i>et al.</i>, (2024)
Competitive-exclusion probiotics	Lactic acid bacteria suppress <i>S. aureus</i> growth in the udder/milk environment.	In vitro / early in vivo	Fernández <i>et al.</i>, (2023)

7. Limitations and Research Gaps

Several caveats temper the optimism that surrounds these emerging strategies. First, the great majority of post-antibiotic approaches discussed above- nanoparticle delivery, AMPs, agr interceptors, and even the most advanced CRISPR-Cas platforms have been validated only in vitro or in murine models; direct evidence in lactating dairy cattle under field conditions remains sparse, and the structural and immunological differences between the murine and bovine mammary gland are non-trivial (**Garmendia-Antoñana *et al.*, 2026**). Second, vaccine efficacy trials have produced genuine-

ly conflicting results depending on challenge strain, vaccine formulation, and outcome measure, and no currently licensed vaccine reliably prevents new intramammary infection (**Middleton *et al.*, 2006; Leitner *et al.*, 2011**). Third, regulatory pathways for approving live biological therapeutics such as bacteriophages in food-producing animals are not yet standardized across major dairy-producing regions, which will likely constrain the pace of commercial translation regardless of underlying efficacy data. Finally, AMR surveillance data are unevenly distributed geographically, limiting the ability to draw global conclusions about

resistance trends from regionally concentrated studies.

8. Conclusion

Bovine mastitis caused by *S. aureus* remains a multifaceted challenge that is unlikely to be resolved by antibiotic therapy alone, given the pathogen's capacity for biofilm formation and intracellular persistence. Diagnostics have advanced meaningfully, with qPCR and emerging CRISPR-based biosensors offering same-day, strain- and resistance-gene-specific information that was unavailable a decade ago. Post-antibiotic therapeutics, phage therapy, phage-delivered CRISPR-Cas systems, nanoparticle delivery, AMPs, and next-generation vaccines represent a genuinely promising but still largely preclinical pipeline.

We identify three priority directions for the field. First, controlled field trials in lactating dairy cattle are needed to determine whether the bactericidal efficacy of phage and phage-delivered CRISPR-Cas systems observed in murine models translates to the bovine udder. Second, harmonized, regionally comparable AMR surveillance combining phenotypic susceptibility testing with genotypic resistance-gene detection would allow the field to move from isolated national reports toward a coherent global picture of resistance trends. Third, given the consistently mixed efficacy of current bacterin vaccines, future vaccine development should prioritize cross-strain protection against the genetically diverse *S. aureus* population circulating in dairy herds, rather than efficacy against a single challenge strain. Progress on these three fronts, alongside continued attention to hygiene and herd management fundamentals, will be necessary to meaningfully reduce the economic and public health burden of this persistent pathogen.

Conflict of Interest

The authors declare no conflict of interest.

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