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Lumpy Skin Disease and Its Diagnostic Insights: A Comprehensive Review

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Abstract

Lumpy skin disease (LSD) is an economically significant, transboundary viral disease of cattle caused by Lumpy skin disease virus (LSDV), a member of the genus *Capripoxvirus* within the family *Poxviridae*. Once confined to sub-Saharan Africa, LSD has spread over the past three decades across the Middle East, Europe and Asia, causing substantial losses in livestock productivity, trade and animal welfare. Transmission occurs predominantly through arthropod vectors, and clinically the disease is characterized by biphasic fever, generalized nodular skin lesions, lymphadenopathy and reduced milk production and fertility. This review outlines the etiology and global epidemiology of LSD, with emphasis on recent advances in laboratory diagnosis, from conventional virus isolation, polymerase chain reaction (PCR) and serology to emerging CRISPR-Cas-based assays, isothermal amplification platforms, high-resolution melting analysis and whole-genome sequencing. Prevention and control, including live attenuated, inactivated and next-generation DIVA-compatible vaccines, are discussed in the context of recombinant strain emergence. The review highlights critical gaps in surveillance and in the validation and lineage coverage of emerging assays, and underscores the need for coordinated global strategies against LSD.

1. INTRODUCTION

Lumpy skin disease (LSD) is a highly infectious, economically significant viral disease of cattle and water buffalo caused by the Lumpy Skin Disease Virus (LSDV), a member of the genus *Capripoxvirus* within the family *Poxviridae* (Gupta *et al*., 2020). Historically confined to African countries, the disease crossed continental boundaries during the last two decades, reaching the Middle East in the early 2000s, southeastern Europe after 2013, and subsequently spreading into several Asian countries including India, Bangladesh, Nepal, Bhutan, China, Vietnam, Thailand, and Indonesia. This rapid geographic expansion has been facilitated by increased animal movement, globalization of livestock trade, climate change influencing vector distribution, and the widespread presence of competent arthropod vectors.

The LSDV is antigenically related to sheeppox and goatpox viruses. Like other poxviruses, LSDV replicates in the cytoplasm of infected cells, forming perinuclear viral factories (Maclachlan and Dubovi, 2010). Its genome is a linear double-stranded DNA of about 151 kbp with a central coding region flanked by 2.4 kb inverted repeats, and it encodes approximately 156 putative genes that share about 97% sequence similarity with goatpox and sheeppox viruses (Tulman *et al*., 2001). Under the electron microscope the virion appears dumbbell-shaped (Moudgil *et al*., 2023).

The morbidity of LSD ranges from 10 to 20%, reaching 45% in some areas, and mortality is usually 1–5% but occasionally higher (WOAH, 2021). The virus is transmitted through direct contact, body fluids such as semen, contaminated surfaces and, above all, arthropod vectors acting mechanically (Sprygin *et al*., 2019b; Liang *et al*., 2022). Biting flies such as *Stomoxys calcitrans* and *Biomyia fasciata* are key vectors (Sohier *et al*., 2019; Issimov *et al*., 2020), and viral DNA has been detected in ixodid ticks from infected calves (El-Ansary *et al*., 2022). Some mosquito species can carry LSDV, but their role in transmission remains uncertain (Chihota *et al*., 2003; Paslaru *et al*., 2022; Li *et al*., 2025). Incidence is higher in the warm, moist summer and autumn months that favor vector breeding (Ahmed *et al*., 2020). The main characteristic of the disease is generalized firm papules and nodules of 0.5–5.0 cm over the body, including the head, neck, udder, legs, scrotum, perineum and buccal

mucosa (Tageldin *et al*., 2014; WOAH, 2021; Sudhakar *et al*., 2020). LSD can be diagnosed on the basis of epidemiology, clinical signs, necropsy findings and molecular and serological tests (Tuppurainen and Oura, 2012), and PCR is a quick and reliable molecular method (Jaferin *et al*., 2022).

LSD is one of the most economically important diseases worldwide. The World Organization for Animal Health (WOAH) makes it a notifiable disease because of the economic impact on livestock sector and high transmissibility across borders (Tadesse *et al*., 2020; Namazi and Khodakaram, 2021). Given the expanding geographic distribution of LSD and the rapid evolution of diagnostic technologies, a comprehensive review of available diagnostic approaches is both timely and necessary. While numerous studies have described individual diagnostic methods and several recent reviews have addressed LSD diagnostics and vaccines (Farag *et al*., 2025; Bhat *et al*., 2025; Sarkar *et al*., 2026; Toker *et al*., 2026), few appraise conventional, molecular, serological, genomic, and emerging platforms against specificity, validation depth, and lineage coverage within a single framework.

2. EVOLVING EPIDEMIOLOGICAL PATTERNS OF LSD: A GLOBAL PERSPECTIVE

LSD was first reported in Zambia in 1929 and became panzootic in South Africa in 1949, affecting about 8 million cattle. It remained largely confined to Africa, with outbreaks in Kenya, Sudan, West Africa and Somalia in 1957, 1972, 1974 and 1983 (Al-Salihi, 2014; Das *et al*., 2021). The disease first crossed into the Middle East with outbreaks in Egypt in 1988 (Ali *et al*., 1990) and Israel in 1989 (Yeruham *et al*., 1995), and was reported again in Israel in 2006 (Brenner *et al*., 2006). Its subsequent spread across the Middle East, Europe and Asia led to its categorisation as a notifiable emerging transboundary disease by the World Organisation for Animal Health (WOAH) (Bhatt *et al*., 2023). LSD was reported in Israel and Turkey in 2012, Jordan and Iraq in 2013, and Iran, Cyprus and Azerbaijan in 2014 (Miranda *et al*., 2016), reached Greece and Russia in 2015 and Serbia in 2016 (Tasioudi *et al*., 2016; Salnikov *et al*., 2018), and entered South and East Asia in 2019, with outbreaks in Bangladesh (July), India (Odisha, August) and China (Sudhakar *et al*., 2020; Das *et al*., 2021; Bhatt *et al*., 2023). Nepal reported its first outbreak in 2020 (Koirala *et al*., 2022), followed by Bhutan, Myanmar, Hong Kong, Vietnam, Sri Lanka and Taiwan (Sudhakar *et al*., 2020; WOAH, 2021). In mid-2022 the disease re-emerged in India in its most severe form yet, with over 155,000 deaths among domestic and wild cattle (Bhatt *et al*., 2023; Kumar and Tripathi, 2022). More recently, LSD was reported in the Republic of Korea (2023) and Japan (2024) and re-emerged in western Europe in 2025, with outbreaks in Italy, France and Spain (Toker *et al*., 2026; Yeşilbağ *et al*., 2026). The timeline in Fig. 1 shows the major outbreaks. The continued spread, driven by legal and illegal cattle trade, animal transport and insect vectors, underscores the need for vigilance and global surveillance.

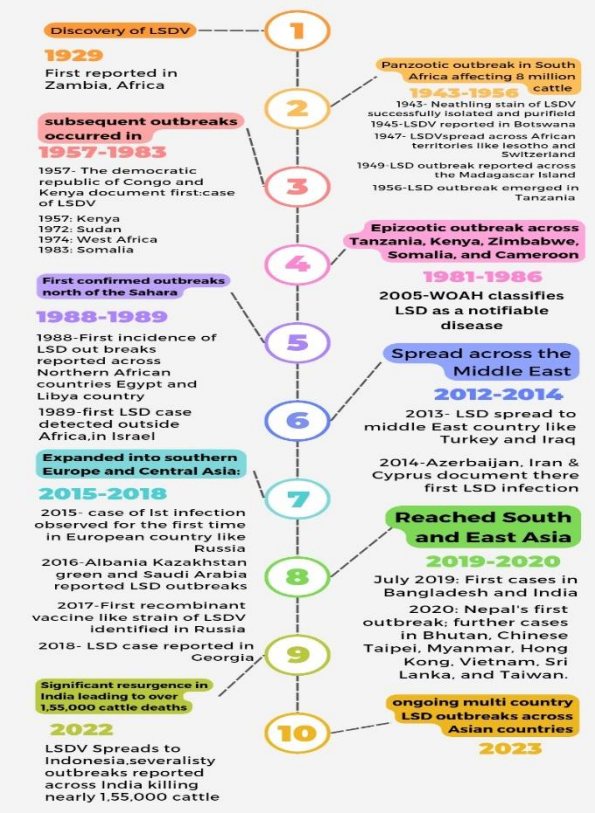


Figure 1- the timeline of major outbreaks associated with LSD

3. DIAGNOSIS

3.1 Clinical specimens

The suitable samples for detecting LSDV include skin lesions, scabs, saliva, nasal swabs, EDTA blood, semen from suspected animals, and whole blood for serum analysis. Post-mortem samples like skin nodules, lung lesions, lymph nodes, and buffy coat are also useful (Tuppurainen, 2017; WOAH, 2021). In chronic cases, LSDV can also be detected in milk and fecal samples (Sharawi and El-Rahim, 2011). Scabs are ideal because they are easy to collect, don't require sedation of animal for collection, can withstand varying temperatures during transport, and contain high virus levels. Full-thickness skin lesion samples can be obtained using a 16-17 mm biopsy punch with local anesthetic. For long-distance transport, tissue samples should be stored in 50% glycerol saline and kept on ice (WOAH, 2010; Tuppurainen, 2017; Saikumar *et al*., 2023a).

3.2 Isolation of LSDV in cell cultures

Isolation and propagation of LSDV in cell cultures play a crucial role in the diagnosis and study of the virus, as well as in the development of vaccines and antiviral therapies. The isolation of LSDV in cell culture involves collecting appropriate clinical samples from infected animals and inoculating them into susceptible cell lines. Various primary and continuous cell lines can support the replication of LSDV, with different cell lines exhibiting varying degrees of sensitivity.

Primary cell cultures such as primary goat testicle (PGT) cells, primary goat kidney (PGK) cells, primary lamb testicle (PLT) cells, and bovine kidney cells are often used. Primary cells are sensitive to LSDV, making them suitable for initial virus isolation (Saikumar *et al*., 2026; Kumar *et al*., 2021; WOAH, 2021). Continuous cell lines such as Madin-Darby Bovine Kidney (MDBK) cells, African Green Monkey Kidney (Vero) cells, and Baby Hamster Kidney (BHK-21) cells can also support LSDV replication (Fay *et al*., 2020; Wang *et al*., 2022). LSDV infection typically leads to characteristic CPEs, such as cell rounding, cell aggregations, vacuole formation, syncytia formation, and detachment of cells. These can be observed within a few days to a week after inoculation (El-Nahas *et al*., 2011; Rashed *et al*., 2023). However, primary cultures are more sensitive compared to continuous cell lines as they closely resemble the natural host cells from which they are derived (Salnikov *et al*., 2018; Kumar and Tripathi, 2022; SaiKumar *et al*., 2023a).

3.3 Isolation of LSDV in embryonated chicken eggs (ECEs)

Isolation of LSDV in chicken embryos is an alternative method for virus propagation and research. The use of embryonated chicken eggs (9- to 12-day-old), particularly the chorioallantoic membrane (CAM), allows for efficient viral replication and can produce characteristic lesions after incubation at 37°C for 5-7 days, that aid in identifying and studying the virus (House *et al*., 1990; Elsheikh *et al*., 2023; Saikumar *et al*., 2026). The lesion in the infected CAM is noticeable with thickening of the membrane over the inoculation site. The viraemic stage is marked by haemorrhage. Furthermore, at the 4th and 5th passage levels, the virus displays virulence by generating necrotic pock lesions of 1-3 mm in diameter, characteristic of pox virus (Wallace *et al*., 1994; Abdallah *et al*., 2018; Elsheikh *et al*., 2023). This isolation of virus in ECE is simplest and cost-effective technique at hand for diagnosis but adaptation of LSDV to ECE is difficult as they were heterogenous.

3.4 Conventional diagnostic techniques

3.4.1 Conventional or real-time polymerase chain reaction (PCR)

PCR is a widely used molecular diagnostic technique for detecting Lumpy skin disease virus. It offers a sensitive, specific, and rapid approach to diagnosing the virus in various sample types, including skin lesions, whole blood, nasal samples, faecal samples, and lymph node tissues (Manjoor *et al*., 2023; SaiKumar *et al*., 2023b; Tuppurainen *et al*., 2005). Specific primers are designed to amplify conserved regions of the LSDV genome. Common target genes include p32 gene (codes for a major structural protein and is highly conserved among *Capripoxviruses*), G-protein-coupled receptor (GPCR) gene, Fusion protein (F) and DNA dependent RNA polymerase 30 kDa subunit (RPO30) genes (Nayakvadi *et al*., 2021; Trinh *et al*., 2022). For more quantitative detection real-time PCR (qPCR) is used, which uses fluorescent dyes (like SYBR Green) or probes that emit fluorescence when the target DNA is amplified. This method allows for real-time monitoring of the amplification process and can quantify viral load (Sprygin *et al*., 2019a; Nayakvadi *et al*., 2021). Species-specific PCR methods can differentiate between LSDV, SPPV and GTPV has been published (Lamien *et al*., 2011). However, PCR is the gold standard test for detecting LSDV, providing reliable tools for diagnosis, epidemiological studies, and monitoring of outbreaks.

3.4.2 Transmission electron microscopy (TEM)

Detection of LSDV by transmission electron microscopy is a direct method that allows visualization of the characteristic poxvirus virion using a negative staining preparation technique (WOAH, 2021). TEM can provide valuable information about the morphology and structure of the virus, making it useful for confirming the presence of LSDV in clinical samples. Suitable samples for detection of LSDV by TEM includes skin biopsies, scabs, or tissue sections from lesions of infected animals. Sometimes, cell culture supernatants containing the virus can also be used. Under TEM, LSDV particles appear as characteristic brick-shaped virions, typical of poxviruses

(Tsai *et al*., 2022; Orynbayev *et al*., 2021). In tissue samples, TEM can also detect viral inclusion bodies, which are areas within cells where viral replication occurs. These appear as dense areas containing viral particles in various stages of assembly (Tan *et al*., 2023).

3.4.3 Histopathological examination

Histopathological examination of skin scabs from cattle infected with LSDV provides insights into the cellular and tissue-level changes caused by the virus. This diagnostic technique helps to confirm LSDV infection by revealing characteristic lesions in affected tissues such as epidermal hyperplasia, ballooning, degeneration, vasculitis, hyperplastic and necrotic hair follicles, haemorrhages in the dermis and the presence of intracytoplasmic inclusion bodies (Tsai *et al*., 2022; Trinh *et al*., 2022; Saikumar *et al*., 2026).

3.4.4 Immunohistochemistry (IHC)

This technique is used to detect specific antigens in tissue sections by utilizing antigen-antibody interactions, which aids in confirming the diagnosis and understanding the extent of viral spread in affected animals. The detection of LSDV antigen in the skin of experimentally infected cattle has been documented by IHC employing F80G5 monoclonal antibody specific for capripoxvirus ORF 057 (Babiuk *et al*., 2008).

3.4.5 Restriction fragment length polymorphism (RFLP)

RFLP is a molecular technique used to detect genetic variations by analyzing DNA fragment patterns produced after digestion with specific restriction enzymes. This is being used to identify and differentiate between vaccine strains from virulent strains of LSDV, based on the unique patterns generated by these enzymes (Menasherow *et al*., 2014).

3.5 DIVA diagnostics for differentiating infected and vaccinated animals

The implementation of large-scale vaccination programs has increased the need for diagnostic tools capable of differentiating infected animals from vaccinated animals (DIVA). Such assays are critical for outbreak investigations, post-vaccination surveillance, and disease eradication programs, particularly in regions where live attenuated capripoxvirus vaccines are routinely employed.

Recent advances have improved the ability to distinguish field and vaccine-derived strains of LSDV. Philips *et al*. (2023) developed and validated a novel DIVA real-time PCR assay capable of differentiating wild-type LSDV strains, including the recombinant Asian strains, from Neethling-based vaccine strains. This assay addresses a significant limitation of earlier DIVA PCR methods, which were unable to reliably identify the Clade 2.5 recombinant strains currently circulating in several Asian countries. The assay provides a valuable molecular tool for outbreak tracing and vaccine monitoring in endemic regions.

In addition to molecular approaches, serological DIVA strategies are also emerging. Using a genome-wide phage-display proteome screening platform, Yuan *et al*. (2025) identified LSDV103 as a promising DIVA antigen. An indirect ELISA based on a truncated LSDV103 recombinant protein (TrLSDV103) demonstrated 100% diagnostic specificity and 86.67% sensitivity for differentiating naturally infected cattle from animals vaccinated with goatpox virus (GTPV). Such assays may provide an effective serological alternative for large-scale surveillance programs. Comparative evaluations of existing serological tests (Krešić *et al*., 2020) and an ORF154-based DIVA-ELISA (Nokhwal *et al*., 2025) have also been reported; however, because capripoxviruses share antigenic determinants, serology remains mainly useful for surveillance and post-vaccination monitoring (Toker *et al*., 2026).

The development of DIVA diagnostics is particularly relevant in countries such as India, where goatpox vaccines are commonly used as heterologous vaccines for LSD control. Under these circumstances, conventional serological assays cannot reliably distinguish vaccine-induced antibodies from those generated following natural infection. Therefore, both molecular and serological DIVA tools are expected to become essential components of future LSD surveillance, control, and eradication programs.

3.6 Isothermal amplification technologies

3.6.1 Loop-mediated isothermal amplification (LAMP)

Isothermal genome amplification techniques like Loop-Mediated Isothermal Amplification (LAMP) offer fast, sensitive, and field-applicable methods for detecting LSDV. They provide practical alternatives to traditional PCR, especially in settings where rapid diagnosis and minimal equipment are essential (Omoga *et al*., 2016). A capripoxvirus-specific LAMP assay has also been described (Das *et al*., 2012).

3.6.2 Recombinase polymerase amplification (RPA)

Recombinase Polymerase Amplification (RPA) has emerged as a rapid and field-deployable molecular diagnostic tool for the detection of lumpy skin disease virus (LSDV). Unlike conventional PCR, RPA operates under isothermal conditions and does not require thermal cycling equipment, making it particularly suitable for resource-limited settings and point-of-care applications. The assay typically functions at temperatures ranging from 37–42°C and can generate detectable amplification products within 15–20 minutes.

Shalaby *et al*. (2016) developed an RPA-based assay for LSDV detection that demonstrated analytical sensitivity comparable to real-time PCR while

significantly reducing assay turnaround time. Subsequently, Zhai *et al*. (2023) validated a real-time RPA assay targeting the ORF132 gene and compared its performance with the WOAH-recommended real-time PCR protocol. Evaluation of 43 clinical samples revealed excellent agreement between the two methods, with a kappa coefficient of 0.94, confirming the suitability of RPA for rapid diagnosis and quarantine station screening. Due to its minimal equipment requirements, rapid amplification kinetics, and high sensitivity, RPA represents a promising alternative to conventional PCR for field surveillance and early outbreak detection. It should be noted, however, that the RPA assays of Shalaby *et al*. (2016) and Jiang *et al*. (2022) do not discriminate LSDV from sheeppox and goatpox viruses (Zhai *et al*., 2023), which limits their use where goatpox vaccine is applied in cattle. Antigen-detection lateral-flow tests for LSDV have also been reported, including a gold-nanoparticle lateral flow test (Abdalhamed *et al*., 2022; reviewed by Bhat *et al*., 2025).

3.7 Advanced molecular diagnostics

Recent advances in molecular diagnostics have revolutionized the detection and characterization of lumpy skin disease virus (LSDV). While conventional polymerase chain reaction (PCR) and serological methods remain the gold standard for LSDV diagnosis (WOAH, 2021; Tuppurainen *et al*., 2005), emerging techniques based on CRISPR-Cas systems, isothermal amplification, and high-resolution melting (HRM) analysis offer superior speed, sensitivity, and field applicability. This section reviews the latest diagnostic innovations that promise to enhance outbreak detection, control, and surveillance capabilities globally, with particular emphasis on point-of-care testing (POCT) solutions suitable for resource-limited settings in endemic regions.

3.7.1 CRISPR-Cas based diagnostic systems

The coupling of isothermal amplification (recombinase polymerase amplification, RPA, or loop-mediated isothermal amplification, LAMP) with CRISPR-Cas nuclease detection has emerged as a major advance in field-deployable LSDV diagnostics, combining rapid amplification with the sequence specificity and collateral cleavage activity of Cas12 enzymes (Jiang *et al*., 2022; Kaminski *et al*., 2021). Three configurations have been described for LSDV. RPA-CRISPR-Cas12a fluorescence assays targeting the LSDV orf068 gene achieve a sensitivity of 5 copies/µL and diagnostic sensitivity/specificity of 96.3%/92.31% on clinical cattle samples, with results in 30–45 minutes using only a heat block and a fluorescence reader or smartphone camera (Jiang *et al*., 2022). LAMP-CRISPR-Cas12a lateral flow assays replace the fluorescence readout with a visual, instrument-free lateral flow strip, enabling completely equipment-free point-of-care testing and simultaneous detection of LSDV alongside related capripoxviruses on a single strip (Yigci *et al*., 2023; Osborn *et al*., 2021). One-pot RPA-CRISPR-Cas12b systems integrate amplification and CRISPR cleavage in a single closed tube, shortening turnaround to about 60–70 minutes, reducing contamination risk, and achieving up to a 100-fold sensitivity gain over RPA alone, with attomolar-level detection reported in proof-of-concept studies (Broughton *et al*., 2020; Li *et al*., 2024).

Collectively, these CRISPR-based platforms offer major advantages over conventional PCR: no thermal cycling, 30–70-minute turnaround versus 2–3 hours, minimal equipment, and dual-layer specificity (amplification plus CRISPR recognition) that reduces false positives, with several formats offering a fully visual or smartphone-based readout suited to farm-level and resource-limited deployment (Hu *et al*., 2022). Current limitations include crRNA instability requiring cold-chain or lyophilized storage, susceptibility of RPA/Cas12 activity to sample inhibitors (blood proteins, soil organics) necessitating further optimization across sample types (milk, semen, hide scrapings), and an immature regulatory pathway that has kept most of these assays at the research or proof-of-concept stage rather than commercial availability (Osborn *et al*., 2021).

3.7.2 High-resolution melting (HRM) PCR for LSDV strain differentiation

High-resolution melting (HRM) PCR uses the differential melting temperature (Tm) of PCR amplicons to distinguish LSDV field isolates from vaccine strains and to differentiate among Capripoxvirus species (LSDV, SPPV, GTPV) in a single closed-tube reaction, without post-PCR manipulation (Pestova *et al*., 2018; Chibssa *et al*., 2019). The assay has been progressively adapted to also resolve the emerging recombinant Asian LSDV strains (Clade 2/2.5) from classical field and vaccine lineages (Menasherow *et al*., 2016; Bhakha *et al*., 2025).

The ORF010 gene (LAP/PHD-finger protein) is the principal HRM target: it is highly conserved within LSDV yet carries sequence polymorphisms between field, vaccine, and recombinant strains that translate into reproducible Tm separations of roughly 0.3–1.0°C, with detection sensitivity comparable to conventional PCR (Pestova *et al*., 2018). Additional validated targets include the B22R gene, whose strain-specific deletions allow four-way differentiation of SPPV vaccine, SPPV field, GTPV and LSDV on one assay (Chibssa *et al*., 2019); the inverted terminal repeat (ITR) region, used to distinguish the Indian Lumpi-ProVacInd vaccine strain from wild-type virus (Kumar *et al*., 2023b); and the EEV gene insertion exploited by Menasherow *et al*. (2016) for vaccine-field discrimination.

HRM PCR's main advantages are its single-step, closed-tube format (amplification and melting in one reaction, 60–90 minutes total), low per-sample cost, and the semi-quantitative viral-load information available from the accompanying Ct value. Its principal limitations are the need for a real-time PCR instrument with HRM capability (precluding field deployment without electricity), the training required to interpret subtle curve-shape differences, and incomplete characterization of Tm

profiles for newer recombinant Clade 2.5 sublineages — a gap partly addressed by a 2025 multi-locus HRM assay from Philips *et al*. that differentiates wild-type, Asian recombinant, and vaccine strains, though broader validation is still ongoing.

3.7.3 Emerging platforms and genomic epidemiology

- Recent advances in microfluidic technology have enabled integration of sample preparation, isothermal amplification, CRISPR detection, and lateral flow readout into a single closed-chip platform, offering complete sample-to-result automation, elimination of contamination through closed-system design, and parallel detection of multiple viral targets (e.g., LSDV, SPPV, GTPV) (Yigci *et al*., 2023; Ghouneimy *et al*., 2023). Such systems remain in development for LSDV specifically, though proof-of-concept platforms exist for related poxviruses. Table 1 summarizes the analytical and operational characteristics of the major advanced molecular diagnostic platforms discussed above.
- Whole-genome sequencing (WGS) complements these targeted assays by enabling complete characterization of the LSDV genome, offering high-resolution insight into strain diversity, recombination, and phylogeographic spread that partial-gene PCR cannot resolve. Since 2017, recombinant LSDV strains arising from co-infection or vaccine-manufacturing processes have driven major epidemics across Russia, Kazakhstan, China, Vietnam, Thailand, Mongolia, and Indonesia (Sprygin *et al*., 2018; Vandenbussche *et al*., 2022; Sprygin *et al*., 2025), and a 2023 complete-genome study traced the global and European dispersal history of these lineages (Van Borm *et al*., 2023). In India, WGS of 2022 outbreak isolates revealed a distinct subclade with a 95-nucleotide deletion in the Functional Resolution Sequence (FRS) repeats that was absent from 2019 strains, and identified two circulating subclades (1.2a and 1.2b), with 1.2b associated with higher morbidity and mortality (Mishra *et al*., 2024). With the growing availability of platforms such as Illumina and Oxford Nanopore sequencing, WGS is expected to become integral to LSD surveillance, supporting real-time outbreak tracking and early detection of recombinant strains. Portable sequencing has begun to be applied to LSDV: hybrid Nanopore-Illumina sequencing of 2022 Indian outbreak isolates identified two co-circulating groups (Yadav *et al*., 2024), and early Indian isolates carry signatures of historical Kenyan KSGP-like strains (Sudhakar *et al*., 2022).

Table 1- comparison of advanced molecular diagnostic platforms for lumpy skin disease virus detection and differentiation

Platform	Turnaround	Equipment	Best Use Case	References
RPA-CRISPR-Cas12a (fluor.)	30–45 min	Heat block + reader	Farm-level outbreak response; rapid clinical confirmation	Jiang *et al*., 2022
LAMP-CRISPR-Cas12a (LF strip)	75–90 min	Heat source only	Remote/field testing; no electricity requirement; POCT	Osborn *et al*., 2021
One-pot RPA-CRISPR-Cas12b	45–60 min	Heat block + reader	High-throughput outbreak screening; enhanced sensitivity	Broughton *et al*., 2020
HRM PCR (ORF010 target)	60–90 min	qPCR with HRM	Laboratory strain differentiation; vaccine-field DIVA	Pestova *et al*., 2018
Multi-locus HRM (recombinant)	70–100 min	qPCR with HRM	Differentiation of Clade 2.5 recombinants from classical strains	Bhakha *et al*., 2025

3.8 Serological diagnostic methods

3.8.1 Enzyme-linked immunosorbent assay (ELISA)

ELISA is used in large-scale epidemiological studies to detect antibodies in cattle populations and to determine the extent of exposure to LSDV. ELISAs for detecting capripox viral antibodies sre commonly used and available as commercial kits (Milovanovic *et al*., 2019; Samojlovic *et al*., 2019). Babiuk *et al*. (2009) developed an indirect ELISA using a Nigerian sheeppox isolate, achieving 96% sensitivity and 95% specificity. LSDV sera showed lower sensitivity (88%) compared to sheep and goatpox sera but maintained the same specificity. Baselli *et al*. (2023) developed various ELISA methods using monoclonal antibodies for the serological diagnosis of LSD.

3.8.2 Virus neutralization

The Virus Neutralization Test (VNT) is a laboratory diagnostic method used to detect the presence

of neutralizing antibodies against the LSDV in serum samples. This test helps in determining whether an animal has been exposed to the virus or has developed immunity, either due to vaccination or natural infection (Haegeman *et al*., 2023). Antibodies against capripoxvirus can be detected 1 to 2 days after clinical signs appear and remain detectable for up to 7 months. To measure these antibodies, either the serum is tested against a fixed amount of virus (100 $TCID_{50}$/well), or a standard virus strain is tested against a fixed dilution of the serum to calculate a neutralization index (WOAH, 2021).

3.8.3 Immuno-peroxidase monolayer assay (IPMA)

IPMA is another test for diagnosing LSD that is both inexpensive and easy to use. It is more sensitive and specific than VNT and commercial ELISA assays (Bedekovic *et al*., 2018). It is particularly useful in serological surveys and research on immunological responses in diseased or vaccinated animals.

3.8.4 Western blot analysis

Western blotting of test sera against capripoxvirus-infected cell lysate offers a sensitive and specific approach for the identification of antibodies to capripoxvirus structural proteins, despite the test being expensive and challenging to do (WOAH, 2021). The technique involves separating proteins based on their molecular weight using gel electrophoresis, transferring the proteins onto a membrane, and detecting specific viral proteins with antibodies. Baselli *et al*. (2023) carried out the western blotting with LSDV positive and negative cattle sera that were diluted 1:20, while antibody binding was detected with an HRP-ruminant IgG Mab (produced from a proprietary hybridoma).

3.8.5 Indirect fluorescence antibody technique (IFAT)

IFAT detects antibodies against LSDV by using fluorescently labeled secondary antibodies. The primary antibodies in the animal's serum bind to the viral antigens, and the secondary antibodies conjugated to a fluorescent dye bind to these primary antibodies. LSDV antigens are prepared by infecting suitable cell cultures with the virus. The infected cells are then fixed on a microscope slide. Under a fluorescent microscope, specific intra-cytoplasmic yellowish-green fluorescent granules were observed in the infected cells, which indicates the presence of LSDV (El-Nahas *et al*., 2011; Rashed *et al*., 2023).

4. CONTROL STRATEGIES

Prevention and control of LSD includes limiting the spread of the virus and protecting livestock. Key measures include:

4.1 Vaccination:

Conventional Live Attenuated Vaccines

Vaccinating cattle with a live attenuated LSD vaccine is the most effective preventive measure. Because LSDV is closely related to sheeppox and goatpox viruses, live attenuated capripoxvirus strains such as the Kenyan sheep and goat pox strain (KS-1), the Yugoslavian RM 65 strain and the Romanian strain are also used. The South African Neethling strain, passaged 60 times in lamb kidney cells and 20 times on the chorioallantoic membrane of embryonated chicken eggs, provides immunity for up to 3 years (Brenner *et al*., 2009; Tadesse, 2020). Effective control requires long-term vaccination with full coverage: new animals should be vaccinated before entering affected farms, calves at 3–4 months if their dams were vaccinated or naturally infected, and breeding animals annually (Tuppurainen *et al*., 2017).

Vaccine Efficacy against Emerging Recombinant LSDV Strains

The emergence of recombinant LSDV strains, particularly the Clade 2.5 lineage circulating in Asia, has raised concern about the effectiveness of existing vaccines. Neethling-based live attenuated and inactivated vaccines induce sustained immunity under controlled challenge (Haegeman *et al*., 2023), and homologous live attenuated vaccines protected cattle against clinical disease after challenge with a recombinant Clade 2.5 strain, although viral shedding was not prevented in all animals (Philips *et al*., 2025).

Recombinant vaccine-like strains may also cause largely subclinical infections that sustain transmission (Shumilova *et al*., 2024), although an experimental study found that clinically affected rather than subclinical cattle were the main source of virus for insect vectors (Sanz-Bernardo *et al*., 2021). Ear-notch and skin-biopsy testing can detect subclinical infection (Aerts *et al*., 2021); vaccination should therefore be complemented by active surveillance, movement control and molecular monitoring.

Next-Generation Vaccine Platforms

Next-generation platforms aim to improve safety, efficacy and DIVA capability. Recombinant subunit vaccines based on the structural proteins ORF075 and ORF090 elicited balanced Th1/Th2 humoral and cell-mediated responses in experimental animals (Gu *et al*., 2025), offering a non-replicating alternative to live vaccines. A recombinant LSDV lacking four virulence-associated genes (LSDV005, LSDV008, LSDV066 and LSDV142) caused no clinical disease in cattle, yet induced neutralizing antibodies and complete protection against virulent challenge (Chervyakova *et al*., 2022).

In India, BIOLUMPIVAXIN, a live-attenuated marker vaccine derived from the Ranchi/2019 isolate, carries an 801-nucleotide deletion in the inverted terminal repeat (ITR) region, as described for the related Lumpi-ProVacInd vaccine (Kumar *et al*., 2023a,b). The deletion allows PCR-based differentiation of vaccinated from naturally infected animals, supporting surveillance and eradication programs.

4.2 Quarantine and movement restrictions: Isolating infected animals and restricting the movement of cattle in and out of affected areas help contain outbreaks (Tuppurainen *et al*., 2017).

4.3 Vector control: Controlling insect vectors, such as flies and mosquitoes that transmit the virus, using insect repellents, insecticides, and fly traps (Tuppurainen *et al*., 2017).

4.4 Biosecurity measures: Implementing strict biosecurity practices, such as disinfecting equipment, vehicles, and personnel, and avoiding sharing equipment between farms (FAO, 2001).

4.5 Early detection and reporting: Monitoring cattle for signs of LSD and promptly reporting suspected cases to veterinary authorities to initiate rapid response actions (FAO, Good Emergency Management Practice [GEMP] 2011).

4.6 Culling: In severe outbreaks, culling infected or high-risk animals may be considered to reduce the risk of further transmission (Miranda *et al*., 2016).

5. KNOWLEDGE GAPS AND RESEARCH PRIORITIES

Despite rapid technical progress, several gaps limit the translation of new diagnostics into routine use. First, specificity has to be interpreted against the vaccine background. The RPA-based assays of Shalaby *et al*. (2016) and Jiang *et al*. (2022) do not discriminate LSDV from sheeppox and goatpox viruses (Zhai *et al*., 2023), and a commercial live-attenuated LSD vaccine was found to contain wild-type LSDV and goatpox-like sequences besides the vaccine strain (Haegeman *et al*., 2021). LSDV-specific and DIVA-compatible assays should therefore be evaluated in cattle vaccinated with homologous and heterologous vaccines. Second, most isothermal and CRISPR-based assays have been tested on small or simulated sample panels, so multi-laboratory validation on naturally infected, subclinical and vaccinated animals is still needed.

Third, the significance of subclinical infection is unresolved. Ear-notch and skin-biopsy testing can detect subclinical infection (Aerts *et al*., 2021), and cattle infected with a recombinant vaccine-like strain remained potential sources of virus (Shumilova *et al*., 2024), yet experimental data implicate clinically affected cattle as the main source for vectors (Sanz-Bernardo *et al*., 2021). Sampling strategies for subclinical and vaccinated herds need standardisation.

Fourth, point-of-care formats are unevenly developed. Lateral-flow antigen tests (Abdalhamed *et al*., 2022; Bhat *et al*., 2025), capripoxvirus LAMP (Das *et al*., 2012) and CRISPR platforms have each been described, but head-to-head comparisons on field samples are lacking, and portable sequencing is only beginning to fill the genotyping gap (Yadav *et al*., 2024; Sudhakar *et al*., 2022). Validation should also extend to lineages that re-emerged in western Europe in 2025 (Toker *et al*., 2026), since several DIVA and HRM tools were designed around Neethling-based vaccines and Asian recombinants (Philips *et al*., 2023; Bhakha *et al*., 2025).

Fifth, guidance is largely restricted to cattle and buffalo, whereas LSDV infection has been documented in camels (Kumar *et al*., 2023c), a giraffe (Dao *et al*., 2022) and Indian gazelles (Sudhakar *et al*., 2023); differential diagnosis of other nodular skin diseases must also be built into workflows (Toker *et al*., 2026). Serological DIVA remains at an early stage because capripoxviruses share antigenic determinants, so serology is mainly useful for surveillance and post-vaccination monitoring, although comparative evaluations of serological tests (Krešić *et al*., 2020) and an ORF154-based DIVA-ELISA (Nokhwal *et al*., 2025) have been reported.

Finally, field evidence should temper enthusiasm for novelty alone. Mass vaccination with the homologous Neethling strain, combined with movement control, was associated with the collapse of epidemics in the Balkans (Klement *et al*., 2020; Calistri *et al*., 2019), although live-attenuated vaccination can cause adverse reactions, including "Neethling disease" (Katsoulos *et al*., 2018), and vaccine quality-control issues have been linked to vaccine-derived recombinant strains (Sprygin *et al*., 2020; Haegeman *et al*., 2021).

6. CONCLUSIONS

In conclusion, LSD poses a significant threat to the livestock industry, with substantial economic and animal health impacts. Comprehensive control and prevention strategies, including widespread vaccination, effective vector management, and stringent biosecurity measures, are essential to curb the spread of the disease. Continued research is crucial for advancing our understanding of the virus, improving vaccine efficacy, and developing innovative control measures. Strengthening global collaboration and surveillance efforts will be key in effectively managing LSD and safeguarding the livestock sector.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

Competing interests

The authors have no competing interest to report.

Author contributions

Saikumar G contributed to data collection, drafting and preliminary reviewing. Avinash P, Manisha M, Likitha N and M Shaz Murtuza were involved in reviewing and editing.

Data availability

Not applicable.

Ethics approval and consent to participate

The authors confirm that the journal's ethical guidelines, as outlined on the author guidelines page, have been followed. Since this is a review article with no original research data, ethical approval was not required.

Consent to publish

Not applicable

Statements and Declarations

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