STAR IDAZ | International Research Consortium on Animal Health

Capripoxvirus Research Review 2015-2026

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Target deliverables of the STAR IDAZ IRC include candidate vaccines, diagnostics, therapeutics, other animal health products and procedures, and key scientific information/tools to support risk analysis and disease control. To achieve these goals, the IRC partners agree to coordinate/align their research programmes to address identified research needs relating to the priority topics and to share results. Research gaps identified by expert Working Groups are organised into research roadmaps for the development of candidate vaccines, diagnostics, therapeutics and disease control strategies, providing a structure to plot identified research gaps and focus future investment (Entrican *et al.*, 2021).

More information on the STAR IDAZ IRC, its mission, partners and previous reports are available on the website https://www.star-idaz.net/

Capripoxvirus Research Review 2015-2026

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of

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Purpose of the Report

Capripoxviruses (CaPV) cause clinically and economically significant transboundary diseases of cattle, sheep and goats, as well as affecting several wildlife species. These diseases are characterised by the development of deep skin lesions, fever and malaise, and are sometimes fatal in severe cases or in susceptible breeds. Hides and wool production may be permanently damaged, gestating foetuses may be aborted, and lactation suppressed. CaPV are notifiable diseases to the World Organisation for Animal Health (WOAH) and their presence within a country necessitates trade restrictions, further spreading their impact in affected areas.

While the geographic range of these diseases is predominantly restricted to Asia, the Middle East and Africa, recent incursions into Europe and increased vector ranges due to climate change are acting together to elevate the risk of global spread.

This report was commissioned at a key juncture in the global CaPV situation to summarise and highlight the most important research published on CaPV between January 2015 and June 2026. Herein we cover advances in knowledge on their fundamental biology, how they may be accurately diagnosed and distinguished in the field, their pathogenesis and determinants of virulence, the immune response to infection and immune evasive strategies, their epidemiology, and new insights into their control, whether by vaccines, anti-microbials or policy.

Equally important, this report also serves to highlight where knowledge is lacking. The information contained within this report is intended to be used to support formal gap analysis that will also incorporate expert opinion and review of current research and control measures, alongside invaluable first-hand “on the ground” knowledge that a review of the literature cannot always capture. It is hoped that the report will be used – together with the outputs of ensuing gap analyses – to rationally inform future funding and policy decisions to combat these devastating diseases.

Limitations of the Report

Through literature searches and expert review, the authors have attempted to consider all eligible literature for consideration, yet it remains possible that some papers may have been missed. Thus, this document should not be considered an exhaustive review of all the literature, rather a summary of those papers deemed to report research of high quality and impact to the field.

To render the document as concise as possible, the authors have limited citation of foundational studies to a minimum, as the readership is assumed to have a solid working knowledge of established research in the CaPV field. Non-specialised readers are referred to published reviews such as that by Hamdi *et al.* (Hamdi *et al.*, 2021b).

Lastly, while the authors have a broad-ranging knowledge of animal pathogens, they are not CaPV specialists. Therefore, this report will highlight the authors' impressions of the current state-of-play and knowledge gaps but will not make any attempt to rank such gaps for importance; this will thus form a key part of future gap analyses.

About the Authors

Dr Lucy Robinson gained her D.Phil. in veterinary immunology from the University of Oxford, UK, and continued her post-doctoral research into exotic infections at the Singapore Immunology Network. Lucy founded Insight Editing London in 2009 and has since successfully assisted with the publication of hundreds of articles and the construction of successful grant applications across diverse scientific fields. Under commission of the STAR IDAZ IRC and the US department of Agriculture she has co-authored/edited research reviews on Animal Influenza (2021), African Swine Fever (2022), Foot-and-Mouth Disease (2023), and Veterinary Mycoplasmas (2023).

Dr Daniel Ackerman completed his Ph.D. in biological sciences and his subsequent post-doctoral studies at Carnegie Mellon University, Pittsburgh, USA. Since then, he has developed advanced communication and editing skills, joining Insight Editing London in 2020. Daniel has assisted with the publication of diverse research articles during his time with IEL, rapidly building his reputation for writing and editing excellence across fields. He also previously authored the STAR IDAZ 2022 African Swine Fever Virus Research Review (2022) and co-authored STAR IDAZ research reviews on Animal Influenza (2021), Foot-and-Mouth Disease (2023), and Veterinary Mycoplasmas (2023).

About the Editor

Dr Jessica Tamanini achieved her D.Phil. in neurobehavioural genetics from the University of Oxford, UK, before undertaking post-doctoral research with the Medical Research Council, UK. She then moved into scientific publishing, first working at Spandidos Publications (London) and then at the Nature Publishing Group (London). She has provided strategic oversight for numerous high-impact commissions at IEL, and directly edited key research reviews on animal pathogens.

Executive Summary

This report combines a comprehensive review of key literature with input from leading scientists across the field (for details of contributors, please see the Acknowledgements) to describe the significant progress made in research into the CaPV causing lumpy skin disease (LSD), sheeppox (SPP) and goatpox (GTP), between 1st January 2015 and June 18th 2026. Herein we provide a literature-based update and summary of notable research, that allows for the identification of some of the areas in which future research and research funding could be targeted for maximum impact and minimum duplication of effort. The priority research areas presented within this report are intended to be used as a tool to supplement future in-depth gap analyses that include additional factors and local/regional considerations.

Despite much work and the important advances in knowledge reported herein, there remains much to be done before these diseases no longer pose a threat to global trade, regional economics and the personal food and income security of livestock keepers whose animals are affected.

Lumpy skin disease virus

The global epidemiological situation concerning LSD is currently tenuous. Lumpy skin disease virus (LSDV), the causative agent of LSD, was already spreading steadily beyond its historical endemic regions in sub-Saharan Africa prior to 1st January 2015, and the time period covered by this report has seen increased transmission speed and geographical range of this spread. Large areas of Africa – including countries with high human and livestock populations such as Egypt, Ethiopia, and Nigeria – continue to suffer substantial economic losses due to LSD. LSD is also endemic across the Middle East and was first detected in many Asian nations during the timeframe covered here: e.g., Russia (2015), China (2019), India (2019), Southeast Asia (2019-2022), South Korea (2023), and Japan (2024). In Europe, regular LSD outbreaks continue to impact cattle farmers in Greece and the Balkans, while a series of outbreaks in France, Italy, and Spain in 2025 highlight the possibility of unexpected LSDV spread via anthropogenic animal movement.

The past decade has seen a great many studies conducted on the transmission routes of LSDV and the risk factors for LSD outbreaks, including anthropogenic factors, insect vectors, environmental and herd management variables, etc. However, much remains unclear, particularly in regard to regional-level factors (different farming practices, native insect species, socioeconomic variables, etc.) that may affect LSDV transmission. Lack of sufficient access to veterinary services, vaccination programmes, and surveillance networks significantly limits our ability to monitor the transmission and mutation of LSDV in rural and/or resource-limited regions. Animal movement and trade networks are particularly common loci of veterinary disease transmission, and focusing surveillance and risk modelling efforts on these networks

can thus prove an effective way to prioritise disease control resources in high-risk areas. The increasing power of computational models has also provided new avenues for estimating transmission and outbreak risks.

Alongside the continuing study of large-scale transmission patterns, efforts are also continuing to characterise the fundamental biology of LSDV and the host-pathogen interactions that define LSD. Continuing advances in genetic sequencing and cell culture/viral isolation technologies have facilitated the generation of increasing numbers of complete viral genomes, providing more complete data compared to single-gene studies and allowing higher-resolution phylogenetic studies to track viral evolution across space and time. Functional analyses of previously uncharacterised LSDV proteins have identified putative virulence factors and immune evasion pathways (e.g., suppression of interferon receptors and interferon-stimulated genes) that could be targeted to reduce the severity of disease and/or promote viral clearance by the host animal. Standardisation (of reagents, experimental techniques, analysis, etc.) remains an important barrier to the practical application of these studies in the field, as substantial differences are often observed between *in vitro* and *in vivo* systems and among different viral strains, host animal breeds, and environments.

While these efforts are underway to clarify the mechanisms of LSDV infection, virulence, and clearance in ruminant hosts, we must continue developing new options for quickly identifying and controlling LSD outbreaks. The clinical presentation of LSD does not allow positive identification without laboratory confirmation, and new diagnostics methods are being developed to reduce the time, labour, and technical expertise required for this. The past decade has seen developments in high-resolution nucleic acid diagnostics (e.g., quantitative polymerase chain reaction, loop-mediated isothermal amplification, and recombinase polymerase amplification assays) alongside serological assays (e.g., enzyme-linked immunosorbent assays [ELISAs]) suitable for rapid detection and large-scale screening.

Meanwhile, vaccination remains our most important asset for LSD prevention and control, and a great many studies published over the last decade have described the development of new potential vaccines and/or the validation of existing ones. Commercial Neethling-derived live attenuated vaccines have generally demonstrated good efficacy and acceptable safety profiles, though lack of standardisation has contributed to high variability among studies. Advances have also been made in the application of LSDV virology/pathology studies to vaccine development (e.g., identifying genes suitable for producing attenuated vaccine strains), and ongoing exploration of inactivated and subunit vaccines have identified promising candidates that maintain protective efficacy while eliminating potential safety risks.

Sheeppox and goatpox viruses

Sheeppox virus (SPPV) and goatpox virus (GTPV) cause diseases of goat and sheep, respectively, with clinical presentations similar to LSD. Mortality rates among infected animals tend to be higher, however, compared to LSD In

large ruminants. SPPV and GTPV are endemic across northern and central Africa, causing regular outbreaks among pastoral and transhumance small ruminant herds across the upper continent. Like LSDV, both viruses are also present in the Middle East and have become endemic in India and Southeast Asia. Outbreaks continue to occur in Russia and China as well. Further west, SPP is endemic in Turkey and causes regular outbreaks in neighbouring European countries. These – along with the sudden reoccurrence of SPP in Spain in 2022, over 50 years after its original eradication in that country – have spurred greater attention to both small ruminant CaPV in western nations.

SPPV and GTPV are both spread primarily through legal and illegal animal movements, with uncertain contributions from insect vectors and wild small ruminant species. As with LSD, one of the most significant barriers to the surveillance and control of these diseases is the lack of sufficient animal monitoring, veterinary care, and vaccination programmes in many affected areas. Ongoing developments in participatory epidemiology and the production of diagnostics and vaccines with less rigid cold chain requirements may assist with these factors, but difficulties persist.

The past decade has seen ongoing characterisation of previously unknown SPPV and GTPV proteins, particularly via comparisons against known analogues in other poxviruses, and the identification of virulence factors involved in viral attachment, apoptosis inhibition, and host immunomodulation. Recent studies have, for instance, begun to map out the viral suppression of host proinflammatory cytokine signalling pathways during early infection, highlighting potential targets for therapeutic development and/or attenuated vaccine strain production. As with LSDV, vaccination is our primary control measure against SPPV and GTPV, and efforts are ongoing to completely characterise existing vaccine strains and develop new ones to address gaps in efficacy, reduce severe side effects, and promote long-lasting protection.

Literature Review and Research Updates by Subject Area

Report approach

The primary literature review was conducted using the applied life sciences CAB Abstracts database (www.cabdirect.org) with search terms specific to the species, pathogens, and date range of interest, starting on 1st January of 2015, until June 18th of 2026. For a full list of the search terms used, please see the Appendices. This approach yielded a total of 1169 papers across the species of interest. Papers were subsequently excluded from further consideration if they were not relevant to the topic or not available in English. The remaining papers were allocated to the following topic areas as shown in Table 1, with papers relevant to multiple diseases being considered for each.

Capripoxvirus/ Research category	Lumpy skin disease virus	Goatpox & sheeppox viruses
Biology of the pathogen	87	42
Geographic distribution and epidemiology	449	165
Immunology	31	9
Diagnosis	87	48
Prevention and control	149	62
Total	**803**	**326**

Table 1: Capripoxvirus peer-reviewed publications, sub-divided by topic area.

These studies formed the main structure of the report and were supplemented by recently published studies retrieved from the PubMed database between March 3rd and June 18th 2026. Additional literature searches were performed during writing to provide appropriate citation for all material and, where needed, useful background. Studies were selected for inclusion based on the authors' impressions of their potential impact within the field and their quality and novelty. More recent studies were given priority within the report. In total, 775 studies, reports and resources are referenced herein.

Introduction

Infections with LSDV, GTPV, and SPPV, comprising the viral genus *Capripoxvirus*, cause economically significant diseases of large (LSDV) and small (GTPV and SPPV) ruminants. In addition to the characteristic skin lesions characteristics of these diseases, they also cause systemic symptoms including lethargy, widespread inflammation, and impaired organ function. These symptoms can cause death in severe cases, and the widely variable morbidity and mortality of CaPV across affected populations can make this severity difficult to predict (Elsheikh *et al.*, 2024; Limon *et al.*, 2020). However, even subclinical infections cause reduced productivity in infected animals, making all three diseases major economic drains on ruminant farming and placing substantial burdens on animal welfare and farmer livelihoods (Guash *et al.*, 2017; Islam *et al.*, 2026; Kenubih *et al.*, 2021; Saqib *et al.*, 2023; Taye *et al.*, 2017).

The current epidemiological situations of the three CaPV are similar: endemicity in Africa, the Middle East, and much of Asia, with periodic outbreaks in Europe that underscore the ability of these viruses to cross large distances via movement of infected animals (reviewed in (Bianchini *et al.*, 2023; Dubey, 2023; Yeşilbağ *et al.*, 2026)). Commercial vaccines are available against the CaPV and are widely used in endemic regions, but critical gaps exist in our ability to monitor the spread of these viruses within rural and remote areas and their transmission to new regions. Disease control programmes are often limited by lack availability of vaccines and/or general veterinary services in endemic areas.

Many aspects of fundamental CaPV biology also remain unclear, including uncharacterised viral proteins and host-pathogen interaction pathways that may determine the course and severity of disease. Meanwhile, lack of standardisation in methodology and data reporting have produced substantial variability in reports of disease prevalence and studies of viral transmission patterns and risk factors. The cost of CaPV outbreaks in endemic regions and the ongoing risk of transmission to currently disease-free regions necessitate a coordinated research and policy response that incorporates all areas of CaPV research. The past decade has brought substantial advances in our understanding of the CaPV and in the development of promising new diagnostic techniques, potential therapeutics, control methods, and vaccine candidates. The purpose of this report is to summarise and present key advances in these fields while highlighting the most important research gaps, aiming to assist researchers and policymakers in establishing the routes of future investigation that may have the largest impact on CaPV management and reduce its economic impacts on livestock farmers and ruminant production systems worldwide.

Lumpy skin disease virus

Introduction

LSD is an expanding transboundary disease of cattle and other large ruminants. Named for its characteristic nodular lesions on the dermal and mucosal surfaces of affected animals, LSD can present with a constellation of diverse and unpredictable symptoms, including fever, lethargy, lameness, and anorexia, alongside impaired liver and cardiac function, pancytopenia, systemic inflammation, and other pathological changes (reviewed in (Haider *et al.*, 2024)). These symptoms can be particularly severe in immunocompromised animals (e.g., lactating cows and newborn calves), and death can occur in severe cases. LSD is typically characterised by variable morbidity and low mortality (~1–3%) (Moudgil *et al.*, 2024); however, mortality levels of ≥25% have been reported under certain outbreak conditions, and even mild cases are associated with reduced animal productivity. LSD-associated losses in milk production, animal growth, and fertility represent a substantial economic burden on affected farmers (Islam *et al.*, 2026; Saqib *et al.*, 2023). In Southeast Asia alone, LSD was responsible for an estimated direct loss of up to 1.45 billion USD (1.07 billion GBP) in the year following its introduction to the region (Roche *et al.*, 2020). Prior to 2021, LSD caused the third most disease cases in cattle, below only echinococcosis/hydatidosis and foot-and-mouth disease (FMD). However, in 2022, LSD became the disease that caused the most cases in cattle, and it retains that status today (Gleason *et al.*, 2025).

LSDV is a double-stranded DNA (dsDNA) virus of the genus *Capripoxvirus*. The other members of the genus are SPPV and goatpox virus, which infect sheep and goats and generally have a host preference (Babiuk *et al.*, 2009). Transmission of LSDV has been reported via insect vectors, semen, and direct contact. The importance of vectors for transmission of LSDV was first demonstrated by lack of LSDV infection in naïve cattle co-housed with experimentally infected cattle displaying clinical LSD (Carn and Kitching, 1995). LSDV phylogeny comprises two major clades, the classical Clade 1 and the recombinant Clade 2, which are further subdivided into subclades 1.1/1.2 and 2.1/2.2 (Xie *et al.*, 2024). LSDV is not thought to have significant zoonotic potential (Velazquez-Salinas *et al.*, 2025), although its genomic material has been detected in the upper respiratory tract of humans living in close proximity to vulnerable ruminants (Tomar and Khairnar, 2024). LSD is a highly contagious disease that has become an increasingly urgent threat to cattle farming worldwide over the past two decades. The first clinical description of LSD came from Zambia in 1929 (Macdonald, 1931). Many outbreaks were observed across the continent in the following decades, and the disease was considered endemic in most sub-Saharan African countries by the second half of the century (reviewed in (Mazloum *et al.*, 2023)). LSD was first reported in Egypt in 1988 and in Israel the following year, and it subsequently became endemic across North Africa and the Middle East. The virus reached Turkey in 2013 and has since spread rapidly across much of the world, reaching the Balkans and Russia in 2015; China, India, and Southeast Asia in 2019; and South Korea and Japan in 2023–2024. It was first reported in France, Italy, and Spain in 2025.

The continuing spread of LSDV, its economic impact in endemic regions, and the threat it poses to currently disease-free areas necessitate a coordinated research and policy framework that integrates new data as rapidly as possible. The past decade has brought substantial advances in our understanding of LSDV biology and evolution, its epidemiology (including the roles of arthropod vectors and anthropogenic factors in transmission), and surveillance and control measures, including improved diagnostics, vaccines, and therapeutics. This section of the report aims to summarise key advances made since 2015 across these areas, collating major lines of ongoing research and supporting researchers and policymakers in directing resources effectively in the fight against LSD.

Literature review

Biology of the pathogen

Proteomics and gene characterisation

LSDV is a CaPV of the family Poxviridae, with a linear, dsDNA genome of approximately 151,000 base pairs (bp) (N. Kumar *et al.*, 2025; Tulman *et al.*, 2001). This genome has been extensively characterised across a wide range of isolates collected at different times and locations, supported by advances in sequencing technologies that have simplified the generation of whole viral genomes (Schlosser-Perrin *et al.*, 2023). Although the number of fully sequenced LSDV genomes has increased substantially in recent years, knowledge of the virus's individual protein components remains relatively limited (N. Kumar *et al.*, 2025). The LSDV genome contains 156 potential open reading frames (ORFs), and the functions of many putative protein products have been inferred through sequence similarity with proteins from other poxviruses (e.g., vaccinia virus) (J. Li *et al.*, 2025; Van Schalkwyk *et al.*, 2022; Y. Wang *et al.*, 2025). Continued characterisation of these proteins, alongside experimental validation of predicted functions, is critical for understanding LSDV biology, virulence, and epidemiology.

Schlosser-Perrin *et al.* conducted label-free shotgun proteomics to identify protein components of the LSDV strain KSGP-0240, reporting 111 viral proteins, of which 66 were considered candidates for packaged viral proteins (Schlosser-Perrin *et al.*, 2023). More recently, an *in vitro* study identified the viral LSDV001 protein as a proinflammatory factor that promotes assembly of the TAK1–TAB2/3 complex, leading to upregulation of interleukin (IL)-1β- and tumour necrosis factor (TNF)-α-triggered signalling (Yang *et al.*, 2025). *In silico* characterisation of the viral protein LSDV132 revealed motifs similar to poxvirus Bcl-2 proteins (Smyth *et al.*, 2026), suggesting a potential role in modulating host cell apoptosis (Sarwar *et al.*, 2024). A comparable bioinformatic analysis of LSDV004 produced similar findings, suggesting a Bcl-2-like protein that may be sensitive to Bcl-2 inhibitors and might play a role in gene regulation and immune evasion (Hasib and

Islam, 2025). Additional insights into putative LSDV gene function have emerged from comparisons with the closely related vaccinia virus (VACV), where multi-omics analyses and structural biology have improved understanding of proteins involved in disruption and evasion of the host immune system (reviewed in (H. Chen *et al.*, 2025)). Meanwhile, experiments in human embryonic kidney (HEK)-293 cells suggest that the LSDV087 protein functions in the decapping of multi-exonic host mRNAs (Z.-Z. Li *et al.*, 2025).

Cell culture and viral replication

Cell culture underpins functional research on CaPV. *In vitro* studies have often been conducted in primary ruminant cells (e.g., lamb testis cells and fetal bovine cells); however, the difficulty of isolating, culturing, and maintaining these cells has driven efforts to identify less labour-intensive alternatives. Madin–Darby bovine kidney (MDBK) cells represent one such alternative and are increasingly used in LSDV research, where they support viral replication and spread *in vitro* (Fay *et al.*, 2020; Nie *et al.*, 2026). Rhazi *et al.* recently reported the development of a diploid cell culture derived from embryonic sheep hearts, demonstrating comparable growth and greater CaPV susceptibility than primary lamb testis cells (Rhazi *et al.*, 2023). Manipulation of primary sheep testis cells has also been explored: transfection of sheep Sertoli cells with the SV40 large T antigen produced an immortalised cell line with suitable properties for CaPV studies (Du *et al.*, 2023). Other cell types reported as permissive to LSDV propagation include baby hamster kidney (BHK-21) cells (van Diepen *et al.*, 2021), ovine lamb heart cells (Kafafy *et al.*, 2023), the human telomerase reverse transcriptase (hTERT)-CSF fetal cow skin and hTERT-bOEC bovine ovarian duct epithelial cell lines (Ma *et al.*, 2023; Ren *et al.*, 2022; H. Zhang *et al.*, 2025), the mouse fibroblast MC3T3-E1 cell line (You *et al.*, 2024), and the human lung adenocarcinoma A549 cell line (Xie *et al.*, 2024). Embryonic sheep skin (ESH-L) cells have also been evaluated as a suitable cell line for CaPV (Rhazi *et al.*, 2021a). MA-104 African green monkey kidney cells were evaluated to isolate LSDV from clinical skin samples and were able to support virus replication similar to goat testes cells (Todkari *et al.*, 2026). The continued development of three-dimensional (3D) cell culture systems, alongside culture media that more closely mimic blood plasma, may further improve the reproducibility and physiological relevance of *in vitro* LSDV studies (reviewed in (Nissanova *et al.*, 2025)).

MDBK cells have been further adapted to enable a broader range of genetic manipulations and support more targeted, in-depth studies of LSDV. Ren and Zhang *et al.* established an MDBK cell line stably expressing the Cre recombinase enzyme, together with a platform for Cre–*loxP* recombination under the control of the VACV early–late H5 promoter, facilitating rapid generation of recombinant LSDV (Ren *et al.*, 2024). Wang and Cheng *et al.* used MDBK cells to investigate LSDV entry pathways, reporting that the virus enters cells via micropinocytosis that is dynamin-dependent but clathrin- and caveolin-independent (S. Wang *et al.*, 2024).

Geographic distribution, epidemiology, and surveillance

As LSDV has continued to spread from Africa across the Middle East and Asia, and more recently into Southeast Asia and Europe, a large number of studies over the past decade have focused on the epidemiology and transmission of LSD in different countries and environments. The production losses and mortality associated with LSD make it a particularly economically significant disease; for example, a recent survey in northern Thailand estimated average per-farm economic losses of approximately 727 USD (~550 GBP) in dairy farms experiencing LSD outbreaks, compared to 349 USD (~265 GBP; primarily related to vaccination and disease prevention) in farms without outbreaks (Modethed *et al.*, 2025).

LSD has a particularly complex global epidemiology that presents substantial challenges for study and surveillance. LSDV evolves relatively slowly (~7.4 x 10^{-6} substitutions per nucleotide site per year, s/n/y), even compared with other dsDNA viruses (average ~5 x 10^{-5} s/n/y) (Sanjuán, 2012; Van Borm *et al.*, 2023; Van Schalkwyk *et al.*, 2022), making phylodynamic analyses and outbreak tracing difficult. Field isolates may differ by only a small number of nucleotide substitutions, often requiring complete or near-complete genome sequencing for accurate epidemiological tracking (Mathijs *et al.*, 2020a, 2020b).

Global situation

Africa

Despite the origin of LSDV in sub-Saharan Africa and its devastating impact on local populations reliant on livestock farming for subsistence and economic security, our understanding of African LSDV phylogeny and epidemiology remains limited (Adedeji *et al.*, 2017; Fadele *et al.*, 2025). LSD prevalence seems to be increasing in many African countries (Hussien *et al.*, 2022; Swiswa *et al.*, 2017), although interpretation of these trends is constrained by inconsistent surveillance and limited standardisation of data collection. In Botswana, for example, LSD was first reported in 1943, yet the first molecular characterisation study of ruminant poxviruses in the country was not published until 2021 (Modise *et al.*, 2021).

Notably few studies of LSD prevalence have been conducted in western and northern Africa despite known disease presence in these regions (Abebaw, 2024; Kadja *et al.*, 2026). Surveillance systems in East Africa seem to be relatively more developed. Molecular analysis of circulating East African LSDV strains showed that 32 of 33 analysed isolates were genetically highly similar, with the exception of a Kenyan field isolate from a vaccinated herd (Embu/B338/2011), which contained a 12-nucleotide insertion in the G protein-coupled receptor (GPCR) gene characteristic of Neethling and KS-1 vaccine strains (Chibssa *et al.*, 2021c).

Ethiopia, which has the largest livestock population in Africa (Chala *et al.*, 2024) and an estimated population-level poverty rate of 39–43% (World Bank, 2025), experiences substantial economic losses associated with endemic LSD (Duguma, 2020; Molla *et al.*, 2017b, 2017c). Spatiotemporal analyses indicate particularly high prevalence following the rainy season (September–December), especially within warm, moist highland regions and in central Oromia (Molla *et al.*, 2017a; Tesfaye *et al.*, 2024). However, comprehensive national studies of LSD epidemiology and control remain limited. Available regional data suggest that current vaccination programmes are unable to sufficiently reduce economic losses, highlighting the need for greater vaccination coverage and efficacy (Dubie *et al.*, 2022; Geletu *et al.*, 2024; Hailu, 2015; Mathewos *et al.*, 2022; Molla *et al.*, 2018, 2017d). A survey of livestock management practices in the Tigray region found that approximately one-third of farmers reported obtaining veterinary services from black market providers, largely due to cultural practices and limited access to formal veterinary infrastructure (Welay *et al.*, 2018).

Tanzania recorded more than 13,000 LSD cases across all 26 regions between 2018 and 2023 (Leopord *et al.*, 2024a), and animal-level seroprevalence of up to 39% has been reported in some regions (Leopord *et al.*, 2024b; Makoga *et al.*, 2024b, 2024a). LSD is also endemic in neighbouring Uganda, where annual outbreaks occur nationwide (Ochwo *et al.*, 2018). A 2019 study of 65 Ugandan cattle herds reported animal- and herd-level seroprevalences of approximately 9% and 72%, respectively (Ochwo *et al.*, 2019). Risk factor analysis identified several animal-level variables, including age and sex, as well as use of communal water sources, as significant factors associated with seropositivity, whereas wildlife contact and introduction of new cattle were not significantly associated (Ochwo *et al.*, 2019). Phylogenetic analysis of circulating strains identified a 12-bp deletion unique to these Ugandan outbreak strains that differentiated their GPCR genes from those of vaccine strains (Ochwo *et al.*, 2020).

Further west, Nigeria, the most populous country in Africa, suffers significant burdens to backyard and transhumance subsistence farmers from LSD (Atai *et al.*, 2021; Gambo *et al.*, 2018; Limon *et al.*, 2020). Infected cattle showed reductions in body weight and milk production of approximately 10% and 65%, respectively, alongside a 60% reduction in slaughter value. Most farmers reported using antibiotics to treat LSD (Limon *et al.*, 2020), increasing per-animal costs and potentially contributing to antimicrobial resistance. Epidemiological studies remain limited, and laboratory confirmation of cases is uncommon (Adedeji *et al.*, 2018; Ifende *et al.*, 2019). Dominant circulating strains appear to have shifted between 2000 and 2010, with more recent isolates showing closer phylogenetic similarity to strains identified in the Balkans during 2015–2016 (Adedeji *et al.*, 2019). A more recent study of isolates from Nigeria, Cameroon, and Benin identified mutations in genes encoding viral envelope proteins, raising concerns regarding immune evasion, vaccine efficacy, and virulence (Fadele *et al.*, 2025). Whole-genome analyses from Sri Lanka, Mongolia, Nigeria, and Ethiopia identified isolates from four previously recognised subgroups, including the “Neethling-like” clade 1.1, clade 1.2.1, the “Kenya-like” clade 1.2.2, and recombinant vaccine-like clade 2 viruses, and additionally identified a novel clade 1.2.3 circulating in west and central Africa (specifically Senegal, Ghana, Nigeria, and Cameroon) (Haga *et al.*, 2024).

LSD is also endemic in Egypt, with particularly high reported prevalence in Upper Egypt and the Nile Delta, including the Monufia and Qalyubia governorates (Awad *et al.*, 2024; Dawoud *et al.*, 2019; Ezzeldin *et al.*, 2022; Keshta *et al.*, 2020). Phylogenetic analyses have indicated the circulation of multiple distinct strains in nearby governorates including Alexandria, Kafr El Sheikh, and Sharqia (Abdallah *et al.*, 2018; Elhaig *et al.*, 2021; Selim *et al.*, 2021). Mortality rates exceeding 6% have been reported in some outbreaks, although the factors underlying this increased severity are unclear (Ali *et al.*, 2021; Elsheikh *et al.*, 2024). Despite regular vaccination of cattle, LSD remains endemic in Egypt, with vaccination failures and recurring outbreaks reported across much of the country (Ata *et al.*, 2026; Rouby *et al.*, 2024, 2021).

LSD was first reported in Algeria in June 2024 (Barberis *et al.*, 2026). This was followed closely by the first reported outbreak of LSD in Tunisia on 7 August 2024, with cases concentrated near the Algerian border (Mejri *et al.*, 2025).

Asia

Asia and the Middle East (including Jordan, Lebanon, Israel, Iraq, and Syria) have experienced a complex pattern of LSDV transmission. Phylogenetic studies have tracked the spread and divergence of viral strains circulating within and across national borders (e.g., in China (Ren *et al.*, 2023; Yao *et al.*, 2025; Yuan *et al.*, 2025), India (Dashprakash *et al.*, 2015; Gupta *et al.*, 2021; Kumar *et al.*, 2023; Srinivas *et al.*, 2023), Iran (Ghalyanchilangeroudi *et al.*, 2021; Hedayati *et al.*, 2021), Pakistan (Manzoor *et al.*, 2023; Nadeem *et al.*, 2025), Russia (Krotova *et al.*, 2022b; Salnikov *et al.*, 2018; Sprygin *et al.*, 2019a), Thailand (Suwankitwat *et al.*, 2023b), and Vietnam (Bich *et al.*, 2024; Truong *et al.*, 2024)), but important gaps remain in our understanding of transmission dynamics and associated risk factors.

LSD was first reported in Iraq in August 2013 (Al-Salihi and Hassan, 2015). The virus has since been detected in cattle, buffaloes, and associated tick populations (Mohammed and Kareem, 2022; Rashid *et al.*, 2017), but our knowledge of LSD epidemiology in Iraq remains limited. Prevalence seems to be higher in rural and peri-urban areas compared with urban areas (Gharban *et al.*, 2019), potentially complicating diagnosis, surveillance, and data collection. LSDV subsequently seems to have spread from Iraq into Iran, which experienced economically significant outbreaks in northwestern provinces in 2014 (Sameea Yousefi *et al.*, 2018).

LSD was first detected in Russia in 2015 (Kononov *et al.*, 2019a), followed by emergence in the western Atyrau oblast of Kazakhstan in 2016 (Mathijs *et al.*, 2020b; Orynbayev *et al.*, 2021; Saltykov *et al.*, 2022), where herd-level prevalence approached 50% 5 years later (Issimov *et al.*, 2022). Between 2015 and 2020, outbreaks in Russia clustered around international borders with Mongolia and China, particularly in smallholder and backyard farms, with annual morbidity and mortality rates of approximately 50–62% and 0–1.2%, respectively (Byadovskaya *et al.*, 2022; Sprygin *et al.*, 2018a). During this period, the virus spread eastward across Russia, with many outbreaks occurring near the borders with Mongolia and the Inner Mongolia Autonomous Region of China (Saltykov *et al.*, 2022; Sprygin *et al.*, 2024). Reports of

LSDV spread into colder Russian regions, where climatic conditions are less favourable for insect vectors, have contributed to ongoing questions regarding transmission routes under different environmental and farm management conditions (discussed in more detail below) (Renald *et al.*, 2023).

Subsequent genetic analyses divided the 2015–2018 Russian outbreaks into two distinct waves. The first (2015–2016) involved field isolates, whereas the second (2017–2018) was characterised by emergence of recombinant "vaccine-like" viruses following introduction of the Neethling-based Lumpivax vaccine in Kazakhstan (Kononov *et al.*, 2020, 2019a; Krotova *et al.*, 2022a; Sprygin *et al.*, 2020; Vandenbussche *et al.*, 2022). A later phylogeographic analysis identified greater biodiversity within these groups than previously recognised, including four subtypes among field isolates and seven among vaccine-like isolates (Saltykov *et al.*, 2021). Recent genomic sequencing from eastern Russia and Mongolia indicates that the LSDV currently dominant in those regions belongs to cluster 2.5 (Sprygin *et al.*, 2025), which is also spreading in Southeast Asia (see below) (Breman *et al.*, 2023; Wibawa *et al.*, 2025). Outbreaks of LSD in Russia occurred between mid-May through mid-November, including weather conditions with snow and freezing temperatures that preclude vector activity (Byadovskaya *et al.*, 2022). It is possible that cases observed in winter occurred earlier due to the long incubation period of LSDV. Furthermore, winter did disrupt LSDV transmission, since there were no reported cases of LSDV between December and April. Despite obvious climatic differences across affected regions, analyses of climatic and environmental variables in Russia identified patterns similar to those observed in India, with risk increasing alongside density of water bodies and monthly precipitation, consistent with greater transmission during warmer and wetter months (Podshibyakin *et al.*, 2024).

The first reported case of LSD in China occurred in Xinjiang, near the China–Kazakhstan border, in August 2019 (Li *et al.*, 2022b; Lu *et al.*, 2021). Genomic analysis of the outbreak strain (LSDV/China/XJ01/2019) identified it as the first representative of cluster 2.5 (Sprygin *et al.*, 2025), with distinct GPCR and RPO30 gene sequences compared to previously identified LSDVs (Ma *et al.*, 2022). The virus showed high similarity to strains subsequently identified elsewhere in China, including China/GD01/2020 in Guangdong province, and across Southeast Asia (Ma *et al.*, 2022; Wei *et al.*, 2023). LSD subsequently spread eastward across China. In 2020, LSDV was identified in Guangdong and Inner Mongolia, and in both cases the responsible strains (MZGD/2020 and NMG/2020, respectively) were later identified as vaccine-like recombinants (Li *et al.*, 2022a; J. Wang *et al.*, 2024b, 2022; Zan *et al.*, 2022). In 2024, Song *et al.* reported the emergence of LSD among yaks (*Bos grunniens*), cattle, and yak–cattle hybrids (dzo) on the Tibetan Plateau(Song *et al.*, 2024). Phylogenetic analysis indicated that the causative strain was more closely related to the India 2022 strain than to earlier Chinese epidemic strains (Song *et al.*, 2024).

LSD was first reported in Nepal in June 2020, after which it spread rapidly among cattle and buffalo populations nationwide (Koirala *et al.*, 2022). A series of outbreaks in 2022 severely affected the country's central Nawalpur district,

with reported morbidity and mortality rates of 28% and 3%, respectively (Pokharel Dhakal *et al.*, 2024). LSD was also reported on Kinmen Island, Taiwan in July 2020 (Tsai *et al.*, 2022).

LSD emerged in India in 2019 and has since caused severe economic losses (Akhter *et al.*, 2025; Gurrappa Naidu *et al.*, 2026; Smaraki *et al.*, 2024). Farm-level prevalence rose rapidly following introduction of the virus; in Uttar Pradesh, for example, reported infections increased more than 19-fold between 2021 and 2022 (Agrawal *et al.*, 2024a). The 2021–2022 outbreak in particular was associated with substantially higher mortality than earlier waves (Alka *et al.*, 2025; Bhatt *et al.*, 2023; Manjunathareddy *et al.*, 2024) and caused estimated losses of approximately 2–2.5 billion USD (~1.5–1.9 billion GBP) (Adari, 2024; Naidu *et al.*, 2025). Genomic studies of the India 2022 strain identified multiple differences relative to the Neethling reference strain and earlier Indian field isolates, supporting the possibility of multiple introduction events (Prabhu *et al.*, 2024; Yadav *et al.*, 2024). A 2022 isolate from Andhra Pradesh additionally contained amino acid substitutions in the viral RPO30 gene that may contribute to increased virulence (Mummidisetty *et al.*, 2025). Spatiotemporal and climatic analyses identified higher humidity and temperature as important regional risk factors (Agrawal *et al.*, 2024b). Although mainland India experienced widespread transmission, the Andaman and Nicobar Islands remained LSD-free until 2021. Subsequent investigation of a 2022 outbreak on Great Nicobar Island identified the causative virus as a cluster 2.5 strain distinct from the cluster 1.2.1 and 1.2.2 viruses circulating on the mainland, suggesting an independent introduction event (Sudhakar *et al.*, 2025a).

LSDV infections have also been confirmed in water buffaloes (*Bubalus bubalis*) in India, where detection of two distinct viral lineages (1.2.1 and 1.2.2) suggested multiple introduction events into the subcontinent (Sudhakar *et al.*, 2025b). The susceptibility of buffaloes to LSDV remains debated, with conflicting reports regarding disease severity; however, one recent study characterised buffaloes as an “accidental non-adapted host” (Di Felice *et al.*, 2024). Additional reports have documented LSDV infection in other ruminants, including mithun (*Bos frontalis*, also known as gayal) (Bayyappa *et al.*, 2025b; Reddy *et al.*, 2024b) and yak (Reddy *et al.*, 2023; Sudhakar *et al.*, 2024).

The first outbreaks in Pakistan were reported in 2021, initially centred in Sindh province before spreading rapidly across the entire country (Ferdoos *et al.*, 2025; Khatri *et al.*, 2023; Saddique and Yousaf, 2024). Mongolia also reported its first outbreak that year in a northeastern region bordering Russia and China (Odonchimeg *et al.*, 2022; Sprygin *et al.*, 2022).

In Southeast Asia, LSD has become one of the most economically significant diseases affecting cattle farming in Bangladesh (Al Mamun *et al.*, 2025; Muktafi *et al.*, 2024; Sayed *et al.*, 2023; Uddin *et al.*, 2022). The disease became endemic following its introduction in 2019 (Ahmed *et al.*, 2025) and was identified as the most prevalent livestock disease in a recent survey of northern Bangladesh (Habib *et al.*, 2024), with estimated losses of approximately 110 USD (82 GBP) per infected cow (Chouhan *et al.*, 2022; Salauddin *et al.*, 2025). A recent epidemiological assessment reported a herd-level prevalence of 15.3% in the study area (the Barishal, Patuakhali, and Chattrogram districts in southern Bangladesh),

with associated risk factors including communal grazing and manure disposal in ponds (Khalil *et al.*, 2026). Whole-genome sequencing of two Bangladeshi strains (BD-V392.1 and BD-V395.1) indicated close relation to the ancestral African Neethling strain (Parvin *et al.*, 2022). More recent genomic analysis identified two distinct circulating clusters: one related to South Asian isolates and another more closely aligned with strains from Africa, the Middle East, and Europe (Tonu *et al.*, 2025).

Vietnam reported its first outbreak in late 2020 (Trinh *et al.*, 2022), and by 2021, phylogenetic analysis of the viral GPCR gene indicated circulation of at least two LSDV variants (Tran *et al.*, 2024). Thailand also reported its first outbreaks in 2021 (Mai *et al.*, 2024; Modethed *et al.*, 2023; Paungpin *et al.*, 2022; Seerintra *et al.*, 2022; Tran *et al.*, 2021) and experienced the highest number of outbreaks in Southeast Asia that year (Maulana *et al.*, 2025a). Initial control measures included animal movement restrictions and closure of live animal markets; however, it was only after the subsequent initiation of a mass vaccination campaign that LSD case numbers began to decrease (Punyapornwithaya *et al.*, 2024, 2023a; Suwankitwat *et al.*, 2022). Thailand became the centre of a propagated regional epidemic that inflicted relatively high morbidity and mortality across the entire region (including Vietnam, Cambodia, Laos, Myanmar, and Malaysia) (Azeem *et al.*, 2022; Vinitchaikul *et al.*, 2023; Wilhelm and Ward, 2023). Early outbreak investigations reported morbidity and mortality rates of approximately 31–40.5% and 0.9–3.5%, respectively (Arjkumpa *et al.*, 2022; Punyapornwithaya *et al.*, 2022; Sariya *et al.*, 2022). Most Thai isolates clustered phylogenetically with recombinant vaccine-like strains previously identified in Russia and China (Singhla *et al.*, 2022; Suwankitwat *et al.*, 2022). In Myanmar, the strain responsible for initial outbreaks in November 2020 was reported to be identical, at least within the extracellular enveloped virion (EEV) glycoprotein gene, to strains circulating in Bangladesh and China (Maw *et al.*, 2022).

Cambodia reported its first LSD outbreaks in domestic cattle in 2021. A single case was additionally identified in banteng (*Bos javanicus*), a critically endangered wild bovine species distributed across Southeast Asia and northern Australia (Porco *et al.*, 2023). This prompted a subsequent vaccination campaign in cattle, banteng, and gaur (*Bos gaurus*), although resource limitations restricted coverage to approximately 21,000 animals (Porco *et al.*, 2023). Malaysia also reported its first LSD case in May 2021, and the disease had spread to 65 of 92 of the country's districts by the end of the year (Saidi *et al.*, 2025).

Singapore documented its first LSD outbreak in March 2022 on a local dairy farm. The responsible strain was genetically similar to circulating variants in Thailand, China, and Russia, supporting ongoing regional transmission (Koh *et al.*, 2025). Indonesia reported its first outbreak in Riau province, Sumatra, later that year (Nugroho *et al.*, 2025a, 2024). Molecular analysis indicated that the causative virus was a recombinant of the Neethling_vaccine_LW_1959 and LSDV_NI-2490 strains (Sendow *et al.*, 2024). LSD continues to spread across the Indonesian archipelago (Hidayat *et al.*, 2025; Murti *et al.*, 2024; Nugroho *et al.*, 2025b) and was first reported on Bali earlier this year (Geary and Robinson, 2026).

Finally, LSD reached South Korea in October 2023, prompting a nationwide vaccination campaign (Ha *et al.*, 2025; Kim *et al.*, 2024). Viral DNA was detected in *Stomoxys calcitrans* stable flies and *Musca domestica* housefly samples collected from infected premises, although viral infectivity and transmission were not analysed (Jeong *et al.*, 2026). Japan experienced its first outbreak in late 2024, involving 22 cattle farms in the Fukuoka and Kumamoto prefectures on Kyushu (Watanabe *et al.*, 2025). Although strict disease control measures successfully limited spread, the risk of reintroduction remains high (Hayama *et al.*, 2025; Watanabe *et al.*, 2025).

Europe

The first outbreak of LSD in Turkey was reported in 2013 (FAO, 2013), leading to the rapid establishment of endemic areas across the country (Albayrak *et al.*, 2018). A retrospective analysis of LSD epidemiology between 2013 and 2021 identified nearly 1,800 outbreaks across 75 of Turkey's 81 provinces, with major circulation hotspots centred in the Aegean, Southeastern, and Eastern regions (Bayir, 2024). Morbidity and mortality associated with these outbreaks varied substantially between geographical regions and cattle herds. A 2018 study in northern Turkey detected LSDV nucleic acid in between 5% (Giresun province) and 66% (Sivas province) of analysed samples, depending on the province (Albayrak *et al.*, 2018). Mat *et al.* applied a susceptible–exposed–infectious–recovered (SEIR) model to analyse the epidemiology and economic impact of the 2019 outbreak in Turkey, reporting an overall prevalence of approximately 4.5%, mortality of 1.1%, and production losses per infected animal of 886 USD (~670 GBP) and 1,067 USD (~806 GBP) for dairy and beef cattle, respectively (Mat *et al.*, 2021).

LSD reached western Turkey in May 2015, after which it continued moving westward at an estimated median rate of 7.3 km/week (Mercier *et al.*, 2018). The introduction of LSD into Greece in August 2015 (Agianniotaki *et al.*, 2017b; Tasioudi *et al.*, 2016) was followed quickly by a series of outbreaks throughout the Balkans (Koleci *et al.*, 2021; Manić *et al.*, 2019; Stojmanovski, 2018), resulting in estimated economic losses of approximately 21 million EUR (~24 million USD; ~18.3 million GBP) in Albania, Bulgaria, and North Macedonia alone between 2016 and 2017 (Casal *et al.*, 2018). Bulgaria was particularly affected during this period but implemented intensive control and surveillance measures that appeared to substantially limit subsequent transmission, as suggested by later studies of ruminant diseases in the Black Sea basin (Arede *et al.*, 2023).

The spread of LSDV across Europe culminated most recently in outbreaks reported in France and Italy in June 2025, followed by Spain in October of the same year (Vinci, 2025; Yeşilbağ *et al.*, 2026). France responded through vaccination of approximately 2 million cattle alongside mass culling of affected herds, measures that were met with protests from some smaller farming unions (de La Hamalde, 2025; Roucaute, 2026).

Modes, routes, and drivers of LSD transmission

The spread and maintenance of LSDV remain subjects of active research, and the predominant modes of transmission are still unclear under many farm, environmental, and ecological conditions ((Sprygin *et al.*, 2019c); comprehensively reviewed in (Bianchini *et al.*, 2023; Haider *et al.*, 2024)). Insects appear to play a predominant role in LSDV transmission (Bianchini *et al.*, 2023; Magori-Cohen *et al.*, 2012), and many species have been identified as potential transmission vectors (Sohier *et al.*, 2019), although conclusive data regarding the role of specific vectors in different environments remain limited. Large-scale studies of disease incidence, transmission patterns, and risk factors must also account for likely underreporting associated with resource limitations and incomplete surveillance systems (Wilhelm and Ward, 2023).

A kernel-based analysis of Thailand's 2021 outbreaks identified a short median herd-to-herd transmission distance (~0.2–0.8 km), suggesting an important role for insect vectors in the epidemiology of LSD within the study regions (Khon Kaen and Lamphun provinces) (Punyapornwithaya *et al.*, 2023b). This was supported by a separate herd-level risk factor analysis from the same period, in which the most significant variable associated with LSD was the absence of herd-level insect management (Arjkumpa *et al.*, 2024). A similar pattern was observed in a retrospective modelling study of outbreaks in Albania during 2016, where most transmission occurred over distances of <5 km (Gubbins *et al.*, 2020).

The proliferation and spread of insect vectors are strongly influenced by increasing temperatures and therefore represent important links between LSD risk and climatic variables (FAO, 2019; Sprygin *et al.*, 2019c). Li *et al.* recently used the biomod2 R package, which integrates several modelling algorithms, to identify environmental variables associated with the distribution of *S. calcitrans* and the mosquito *Aedes aegypti* (L. Li *et al.*, 2025). Distribution of the stable fly was primarily associated with managed pasture coverage and precipitation seasonality, whereas *Ae. aegypti* was more strongly influenced by urban land cover and temperature-related variables. The researchers also combined these analyses with climate projection data from the World Climate Research Programme to estimate future expansion of these vectors under climate change scenarios. Although projections varied depending on the model used, expansion of vector ranges appeared inevitable; the selected model predicted approximately 96% and 44% increases in the geographical ranges of *Ae. aegypti* and *S. calcitrans*, respectively, over the next 25–30 years (L. Li *et al.*, 2025).

Disease severity, perhaps as a property of host immune response, may also influence vector-mediated transmission. Sanz-Bernardo *et al.* quantified viral acquisition by several insect vectors, including *S. calcitrans* and *Ae. aegypti*, following blood feeding on LSDV-inoculated cattle, and reported that insects feeding on subclinically infected animals were 97% less likely to acquire LSDV compared with those feeding on clinically affected animals (Sanz-Bernardo *et al.*, 2021). However, transmission from subclinically infected cattle has still been observed experimentally (Shumilova *et al.*, 2024a),

and a more recent study showed that *S. calcitrans* was capable of transmitting LSDV from subclinical donor cattle to two of five naïve recipient animals (Haegeman *et al.*, 2023c).

Sanz-Bernardo *et al.* also calculated vector-specific viral reproduction numbers (R_0) and viral retention times, both of which were highest for *S. calcitrans* (19.1 and up to 8 days, respectively) (Sanz-Bernardo *et al.*, 2021). These findings broadly aligned with earlier work identifying *S. calcitrans* as the most efficient known insect vector of LSDV, followed by *Ae. aegypti* (Gubbins, 2019). High relative abundance of *S. calcitrans* has also been associated with increased numbers of outbreaks on Israeli dairy farms (Kahana-Sutin *et al.*, 2017).

In 2025, Sri-in *et al.* published the first report of experimental transovarial transmission of LSDV in *Ae. aegypti* infected with high viral loads (Sri-in *et al.*, 2025), indicating that the mosquito may be a vector of LSDV in the wild. Mosquitoes can acquire substantial viral loads from cutaneous lesions on clinically affected animals, supporting their role as mechanical vectors (Sanz-Bernardo *et al.*, 2022).

Although *Ae. aegypti* is the most widely studied mosquito vector of LSDV, *Culex tritaeniorhynchus, Culex quinquefasciatus*, and *Aedes albopticus* have also demonstrated susceptibility under experimental conditions (Riana *et al.*, 2026, 2024). Retention of LSDV following blood feeding has additionally been reported in *Aedes japonicus*, *Culex pipiens*, and the biting midge *Culicoides nubeculosus* (Paslaru *et al.*, 2022), while horsefly (*Haematopota*) species have also been shown to support mechanical transmission (Sohier *et al.*, 2019). LSDV DNA had previously been detected in *Culicoides punctatus* midges in Turkey (Şevik and Doğan, 2017).

LSDV has also been detected in additional fly species, including flesh flies (*Sarcophaga* spp.) in Cameroon (Fadele *et al.*, 2025) and the non-biting flies *M. domestica* and *Muscina stabulans* in China (Y. Wang *et al.*, 2022).

In addition to mosquitoes and biting flies, ticks have also been implicated in LSDV epidemiology as potential reservoirs of the virus. Following initial detections of LSDV in hard ticks, Tuppurainen *et al.* attempted viral culture in *Rhipicephalus* tick cell lines; although replication did not occur, the virus remained infectious *in vitro* for 35 days at 28°C (Tuppurainen *et al.*, 2015). A survey of ticks collected from livestock in western Kazakhstan detected LSDV DNA in approximately 14% of *Dermacentor marginatus* ticks and 6% of *Hyalomma asiaticum* ticks (Sultankulova *et al.*, 2022), and *Hyalomma anatolicum* has demonstrated both intra-stadial and transovarial transmission under experimental conditions (Ali *et al.*, 2024). In Egypt, LSDV has been isolated from *Rhipicephalus annulatus* ticks collected from LSD-infected cattle in the Kafr El Sheikh and Beheira Governorates (El-Ansary *et al.*, 2022) and the Beni Suef Governorate (Abdelbaset *et al.*, 2022; Rouby *et al.*, 2017), and these ticks seem to have a role in LSDV transmission between and among cattle and buffaloes (Zeedan *et al.*, 2024).

Other transmission routes remain less well understood. Nesterov *et al.* demonstrated that the recombinant vaccine-derived strain Udmurtiya/2019 could be transmitted indirectly between experimental animals housed in an insect-proof facility, raising questions regarding the role of viral mutations in facilitating alternative transmission routes (Nesterov *et al.*, 2022). LSDV also seems capable of long-term environmental persistence and overwintering in cold climates (Shumilova *et al.*, 2022a). Previous studies have shown that LSDV can be shed and transmitted through semen, but the practical implications of this transmission route in the field are unclear (Annandale *et al.*, 2018; Givens, 2018; Kononov *et al.*, 2019b; Sudhakar *et al.*, 2020). A suspected case of intrauterine transmission has also been described (Rouby and Aboulsoud, 2016). Meanwhile, Shumilova *et al.* described the first evidence of alimentary LSDV transmission, reporting that inoculation of feed with the vaccine-like recombinant strain Saratov/2017 led to low-level viral infections in two out of five experimental bulls (Shumilova *et al.*, 2022b). In India, LSDV genomic material was detected in semen of naturally infected bulls up to 235 days post-onset of clinical signs in one bull and up to 175 days in four others (Sudhakar *et al.*, 2026).

Studies examining outbreak-associated risk factors provide insight into the environmental, farm management, and animal-level conditions associated with LSDV transmission. Many groups have used logistic regression approaches to identify key outbreak-associated risk factors in different regions (e.g., (Abera *et al.*, 2015; Bayyappa *et al.*, 2025c; Hasib *et al.*, 2021; Sethi *et al.*, 2022)). The continued development of computational modelling approaches, including machine learning, has provided new opportunities for predicting transmission pathways, outbreak probabilities, and risks of introduction into naïve regions ((Gouda and Abdallah, 2025); reviewed in (Renald *et al.*, 2023)). However, identified risk factors can vary considerably depending on study design, selected variables, and analytical methodology—even in geographically similar regions such as the Punjab areas of India and Pakistan (Alka *et al.*, 2025; Jabbar *et al.*, 2025).

Kiplagat *et al.* identified cattle breed (exotic/European versus indigenous) and the source of replacement stock (external versus within-herd) as the primary risk factors associated with outbreaks in Nakuru County, Kenya (Kiplagat *et al.*, 2020). Accordingly, herds composed entirely of exotic breeds also experienced greater estimated financial losses associated with reduced milk production and treatment or vaccination costs (Kiplagat *et al.*, 2020). Similar findings have been reported in more recent studies from Pakistan (Memon *et al.*, 2025; Saqib *et al.*, 2023) and Iran (Isapour *et al.*, 2021), where indigenous cattle seemed less susceptible to LSD-related morbidity and/or mortality than exotic breeds.

Climatic and ecological variables also appear to contribute substantially to LSDV transmission, although their precise relative importance is difficult to quantify. In a comparative study of livestock diseases in the Sahelian, Sudano-Sahelian, and Sudanian climate zones of Burkina Faso, Sanou *et al.* reported that LSD outbreaks were associated with the occurrence of cold and wet days (Sanou *et al.*, 2025). A study in Bangladesh identified seasonal peaks between May and November and found correlations with rainfall, relative humidity, minimum temperature, and wind speed (Ahmed *et al.*, 2025). Similar patterns were reported by Gomo *et al.* in a retrospective spatiotemporal study of LSD outbreaks between

2000–2013 in the Mashonaland West Province of northern Zimbabwe (Gomo *et al.*, 2017), where outbreak numbers were associated with higher temperature, increased rainfall, and proximity to game areas and regions frequently vaccinated against foot-and-mouth disease (Gomo *et al.*, 2017).

Li *et al.* conducted a spatiotemporal analysis covering the spread of LSD across the entire Asian continent between 2012 and 2022 using a maximum entropy (MaxEnt) ecological niche model to predict areas at particular risk of outbreaks (Li *et al.*, 2023). Five environmental and farm management properties (namely cattle density, land cover, isothermality, buffalo density, and maximum temperature of the warmest month) accounted for more than 90% of the model contribution, with highest predicted risk across the Caucasus, the Levant, southern India and Sri Lanka, and much of Southeast Asia (Li *et al.*, 2023). Applying similar methodology at a global scale and incorporating the vectors *S. calcitrans* and *Ae. aegypti*, the same group generated predicted suitability maps highlighting much of Europe, the eastern United States, and southeastern South America (An *et al.*, 2023). These findings aligned with earlier MaxEnt analyses of eastern Europe (Machado *et al.*, 2019). More recently, Maulana *et al.* conducted MaxEnt modelling of environmental suitability for LSD in Thailand, and identified the northeastern and central regions of the country as particularly high-risk due to a combination of land cover, cattle density, and vegetation density (Maulana *et al.*, 2025b).

Finally, serological studies have confirmed the presence of anti-LSDV antibodies in several wild ruminant species in Africa, but the potential roles of wildlife in the transmission, maintenance, and re-emergence of the virus remain unclear (Gortázar *et al.*, 2022; van Vuuren and Penzhorn, 2015). LSDV has been detected in common eland (*Taurotragus oryx*), springbok (*Antidorcas marsupialis*), and impala (*Aepyceros melampus*) (Molini *et al.*, 2021; Van Schalkwyk *et al.*, 2024). As the virus expands into new regions of Asia and Europe, additional wildlife species are likely being exposed, highlighting the need for further investigation. In 2022, LSDV was isolated from a giraffe (*Giraffa camelopardalis*) that died in a zoo in northern Vietnam (Dao *et al.*, 2022). While past research had demonstrated experimental LSDV infection of giraffes (Young *et al.*, 1970), this finding represented the first documented case of natural transmission. The virus was later detected in samples from a wild giraffe in South Africa (Van Schalkwyk *et al.*, 2024). Another first-in-species report came from India, where Kumar *et al.* identified a PCR- and serology-confirmed case of clinical LSD in a camel (*Camelus dromedarius*) (R. Kumar *et al.*, 2023b). Meanwhile, Sudhakar *et al.* reported a rare case of LSD-associated mortality in free-ranging Indian gazelles (*Gazella bennettii*) in Rajasthan, India; two animals with characteristic skin lesions were captured and quarantined, but both died within 3 days (Sudhakar *et al.*, 2023).

Surveillance

Established surveillance networks have recently been complemented by open-source data gathering and analysis tools. For example, the "EPIWATCH" system was recently employed to track LSD outbreaks in South and Southeast Asia, combining official reports with online resources to identify early warning signals and help circumvent delays in reporting to WAHIS (Hutchinson *et al.*, 2024). Pruvot & Denstedt *et al.* described the development and implementation of WildHealthNet, a One Health-aligned wildlife disease surveillance initiative for low- and middle-income countries (LMICs) that incorporates participatory epidemiology and national-scale event-based disease reporting (Pruvot *et al.*, 2023). Among other wildlife-associated pathogens, the researchers trialled this system for surveillance of LSD in wild banteng (*Bos javanicus*) in Thailand, where rapid communication between local community rangers and regional disease reporting networks facilitated faster outbreak responses (Pruvot *et al.*, 2023). Strong communication pathways between veterinarians, researchers, and local- and national-level animal health authorities are also critical for effective surveillance, particularly in regions at high risk for the introduction and spread of infectious diseases (Motta *et al.*, 2019).

A few studies have focused on validation of sample collection and analytical approaches for LSD surveillance. Baselli *et al.* evaluated competitive and indirect enzyme-linked immunosorbent assays using more than 1,200 European serum samples from naturally infected, experimentally infected, vaccinated, and field-negative cattle, reporting specificity and sensitivity values of ≥0.95 and 0.87–0.94, respectively, relative to the virus neutralisation test (Baselli *et al.*, 2025). Diagnostic accuracy declined in animals that had received only a single vaccination or were sampled 5 months post-vaccination (Baselli *et al.*, 2025), highlighting that blood sampling is not always optimal for LSDV detection and that timing of sample collection is an important consideration in seroprevalence studies (Gupta *et al.*, 2025). Group-level oral fluid sampling has also been successfully used for LSDV detection by quantitative polymerase chain reaction (qPCR) from two to 28 days post-experimental infection (Dietze *et al.*, 2018). Environmental sampling approaches, including swabbing with electrostatic dust cloths, represent another relatively simple and low-cost strategy for surveillance in rural areas (Brown *et al.*, 2024).

Finally, important efforts are underway to standardise, simplify, and streamline the collection and reporting of LSD outbreak data, including the ongoing SIGMA initiative coordinated by the European Food Safety Authority (EFSA, 2019, 2018; EFSA *et al.*, 2019).

Diagnosis

LSD cannot be identified accurately based solely on clinical signs, which overlap with several other diseases, and instead requires laboratory confirmation. Established molecular techniques are available to detect the viral genome, including polymerase chain reaction (PCR), real-time PCR and Loop-mediated isothermal amplification (LAMP). Alongside, the gold-standard virus-neutralisation test (VNT) and ELISA use serological approaches, while direct virus isolation (VI), pathology to detect intracytoplasmic inclusion bodies and immunohistochemistry for CaPV antigen are also widely accepted as reliable and sensitive. The WOAH lists currently validated diagnostic tests and the reader is referred to this resource for further details on those approaches (WOAH, 2025). However, many of these techniques are also labour-intensive, require technical expertise, and can be costly and time-consuming. In settings where resources are limited and rapid results are required, newer approaches may offer equivalent sensitivity and specificity while being easier, faster and cheaper to perform.

Nucleic acid-based diagnostics

Conventional PCR, quantitative real-time PCR, and high-resolution melting (HRM) assays are all rapid and sensitive methods for LSDV detection. Over the past decade, these techniques have been further optimised, adapted to specific applications, and advanced towards use in low-resource settings.

Quantitative PCR

A team working at Plum Island reported successful modification of two established qPCR diagnostic tests for CaPV. The Balinsky approach detects *ORF068*, while the Bowden method detects *ORF074*; by exchanging the PCR kit used for the Balinsky method and both the thermocycler and PCR kit for the Bowden assay, sensitivity improved from 82% to 92% and from 58% to 82%, respectively (Das *et al.*, 2017).

Wen *et al.* (2023) devised a real-time qPCR method for identifying CaPV in cattle, sheep, and goats based on detection of the conserved CaPV 32 gene. The assay demonstrated 100% specificity and sensitivity and showed superior performance to the current SYBR Green-based PCR recommended by the World Organisation for Animal Health, alongside the operational advantages associated with qPCR compared with conventional PCR (Wen *et al.*, 2023).

Similarly, Nan *et al.* (2023) developed a triplex real-time qPCR able to detect and distinguish LSDV, GTPV and SPPV in a single reaction, with a sensitivity of 5.41, 27.70, and 17.28 copies/µL, respectively; importantly, in cases of mixed infection, the novel assay accurately detected the two or three viruses in the experimental sample, and also performed well with field samples (Nan *et al.*, 2023)

An alternative strategy to address the time- and equipment-intensive nature of PCR diagnostics is ultra-fast qPCR. Cao *et al.* (2023a) reported the development of such an assay, leveraging the clustered regularly interspaced short palindromic repeats (CRISPR)–CRISPR-associated protein 12a (Cas12a) system to generate accurate results in under 30 minutes, with a detection limit of 2,500 copies per µL (comparable to conventional PCR) and outputs detectable via fluorescence or lateral flow (Cao *et al.*, 2023a).

CRISPR–Cas12a technology may also enhance the sensitivity of qPCR-based detection of LSDV. A study conducted in China in 2022 used PCR or recombinase-aided pre-amplification to reduce the limit of detection to a single copy per reaction, producing a highly sensitive assay that specifically detected LSDV (but not sheep pox virus (SPPV) or goat pox virus (GTPV)) within approximately 5 hours (Liao *et al.*, 2022). Similarly, Cao *et al.* (2024) employed a triple amplification strategy incorporating recombinase polymerase amplification (RPA), CRISPR–Cas12a, 10–23 DNAzyme, and Baby Spinach RNA aptamer, resulting in an assay that was 100 times more sensitive than RPA with Cas12a alone and achieved 100% diagnostic accuracy in 50 field samples (Cao *et al.*, 2024).

In 2023, Sprygin and colleagues developed a real-time PCR assay targeting ORF LW032 that enabled specific detection of Kenyan sheep and goat pox (KSGP)-related isolates of LSDV and recombinant strains containing the KSGP backbone (Sprygin *et al.*, 2023a). This represents an important tool for distinguishing these cluster 1.1 viruses from cluster 2.5 recombinant LSDV strains in regions where both may co-circulate.

Efforts to develop mobile real-time PCR assays have also progressed. Armson *et al.* (2017) reported a portable system with comparable or improved performance relative to laboratory-based PCR for detecting SPPV, GTPV, and LSDV across a range of sample types, delivering results within 1 hour (Armson *et al.*, 2015).

Simplified DNA extraction methods are also critical for expanding access to molecular diagnostics. TripleE (easy express extraction), developed at the Friedrich-Loeffler-Institut in Germany, enables nucleic acid isolation from up to eight samples within approximately 10 minutes at either the pen-side or in a minimally equipped laboratory (Korthase *et al.*, 2022).

Loop-mediated isothermal amplification (LAMP)

Building on foundational work by Batra *et al.* (2015) targeting P32 (Batra *et al.*, 2015), several studies have explored the practical advantages of LAMP for facilitating LSDV detection in low-resource settings.

Balnod *et al.* (2025) developed a portable visual LAMP assay capable of diagnosing LSDV within 1 hour from blood, nasal swabs, or serum samples. The LSDV Solid-state Visualization Detection Kit (Hebei Normal University of Science and

Technology, China) demonstrated 100% positive and negative predictive values (albeit with only four positive samples among 32 tested), as well as 100% diagnostic sensitivity and specificity (Balnod *et al.*, 2025). These results are comparable to earlier LAMP assays evaluated in Thailand during the 2021 outbreak (Laohasatian *et al.*, 2023) and in Iran in 2024 (Edrisi *et al.*, 2024), and markedly improved relative to the prototype LAMP assay reported by Macharia *et al.* (2024), which showed lower sensitivity (60%) and specificity (86%), with a kappa value of 0.32 compared with the reference qPCR method (Macharia *et al.*, 2024).

Recombinase polymerase amplification (RPA) assay

RPA is an isothermal amplification technique that eliminates the need for a thermal cycler and can be performed in as little as 30 minutes at ambient temperature. The addition of a specific fluorescent probe enables real-time monitoring, as seen in real-time RPA assays.

Advances in portable RPA technology with high sensitivity and specificity have been reported throughout this review period. Building on early work by Shalaby *et al.* (Shalaby *et al.*, 2016), Zhai *et al.* used RT-RPA targeting the ORF132 gene to distinguish samples from LSD-affected cattle from those vaccinated with AV41 GTPV. The assay demonstrated a limit of detection of 15 copies/µL, with sensitivity and specificity of 97% and 100%, respectively, and a kappa value of 0.94 compared with conventional RT-PCR across 43 field samples (Zhai *et al.*, 2023).

A similar approach combining RPA with a CRISPR–Cas12a fluorescence assay targeting ORF068 also showed strong performance, detecting as few as five copies per µL in spiked samples and performing comparably to qPCR in a field evaluation involving 40 samples from affected or healthy cattle (Jiang *et al.*, 2022).
Another study employed RT-RPA with a lateral-flow readout targeting the conserved CaPV p32 gene. This method showed equivalent specificity to RT-PCR and RT-RPA but achieved a 10-fold lower detection limit in spiked samples and produced accurate results from field samples within 25 minutes (Liu *et al.*, 2023).

RPA has also been used to differentiate between the three CaPV species despite their approximately 97% nucleotide homology. Cao *et al.* (2023b) combined CRISPR–Cas12a with multiplex RPA to distinguish SPPV, GTPV, and LSDV through simultaneous detection of VARV B22R and RPO30 genes. The assay demonstrated high sensitivity and specificity, with detection limits of 40, 60, and 50 copies, respectively, and produced easily interpretable lateral-flow outputs (Cao *et al.*, 2023b).

Nanopore sequencing

Advances in portable sequencing technologies have enabled the “lab in a suitcase” model for field diagnostics, previously demonstrated for avian influenza virus detection (Abd El Wahed *et al.*, 2015). Eltom *et al.* (2021) demonstrated the application of nanopore sequencing for diagnosis and differentiation of CaPV infections in field settings. Both whole-

genome and RPO30 sequencing approaches achieved 98% specificity and enabled accurate diagnosis within 2 hours, whereas P32 and GPCR targets were less suitable (Eltom *et al.*, 2021).

Real-time high-resolution melting (HRM) PCR

The potential for HRM PCR to distinguish infections caused by different poxviruses was noted almost ten years ago (Gelaye *et al.*, 2017). Based on genetic variation in the LSDV ORF010 sequence, Pestova *et al.* (2018) showed that HRM PCR can differentiate samples containing SPPV, GTPV, and either field or Neethling-related vaccine strains of LSDV. The method was also capable of detecting vaccine-derived LSDV in insect vector samples (Pestova *et al.*, 2018).

Protein diagnostics

One study reported an alternative approach to LSDV diagnosis based on direct detection of viral proteins using molecularly imprinted synthetic polymers, which are engineered to recognise and bind specific target molecules. Kassem *et al.* (2024) described a nitrocellulose paper-based fluorescent MIP sensor for detecting LSDV in virus-spiked samples of blood, serum, and skin nodule lesions. The sensor demonstrated sensitivity comparable to RT-PCR and high specificity in distinguishing LSDV from other bovine viruses tested (Kassem *et al.*, 2024).

Serological assays

Serological assays are important for large-scale screening to support outbreak monitoring, vaccination programmes, and the establishment of disease-free status, yet developing inexpensive and easily executed options has been challenging. In 2017, a commercially available ELISA was launched by ID.Vet known as the ID Screen® Capripox Double Antigen Multi-species ELISA kit (hereafter, "the ID-Vet ELISA"), which performs well in cattle in some settings but is limited by detection of antibodies only several weeks after infection or vaccination (and in some cases not at all in subclinically infected animals or low vaccine responders). It has also been reported to show low sensitivity under field conditions and may be prohibitively expensive in some contexts. The VNT assay is well-established but requires the use of live virus, a high-containment laboratory, and highly trained technical staff, precluding its use in many settings.

ELISA

Although many studies report the development of in-house ELISAs for detecting antibodies against LSDV, most offer, at best, comparable performance to the ID.Vet ELISA. These include assays based on P32 (LSDV 74) cloned from a local Kazakh isolate of LSDV (Tursunov *et al.*, 2023), an indirect ELISA that underperformed relative to the commercial assay (Sthitmatee *et al.*, 2023), the P32-based indirect ELISA developed in Iran (Ebrahimi-Jam *et al.*, 2021), and an ELISA based on detection of antibodies to recombinant F13L that was developed in Thailand (Angsujinda *et al.*, 2025).

Among the studies that report improved performance or practicality/accessibility over the commercially available assay are the work of Berguido and colleagues (2022). The group developed an indirect ELISA based on the VACV C-type lectin-like protein A34 (LSDV 123) (which performed better than the extracellular enveloped virus glycoprotein A36), achieving sensitivities and specificities of 99% and 99% for LSDV, and 98% and 95% for SPPV and GTPV, respectively, using serum from VNT-positive experimentally challenged animals (Berguido *et al.*, 2022). Similarly, Baselli *et al.* (2023) described two novel monoclonal antibodies fur use in an ELISA that showed comparable sensitivity to the ID.Vet ELISA and VNT in detecting seroconversion to LSDV in experimentally infected cattle, while offering improved detection of antibodies against SPPV and GTPV (Baselli *et al.*, 2023). Another study completed around the same time reported similar sensitivity in an ELISA using recombinant A27L and L1R (Ntombela *et al.*, 2023).

A competitive ELISA based on the LSDV A33R (LSDV 122) antigen and anti-A33R polyclonal antibody demonstrated 96% sensitivity and 99% specificity for CaPV in serum samples from experimentally or field-exposed, confirmed positive cattle, supporting its potential for high-throughput, cost-effective sero-surveillance at the herd level (Chen *et al.*, 2024). Similarly, a double antigen sandwich ELISA using A33R achieved a diagnostic sensitivity of 94.7% and a specificity of 96.3% across confirmed positive CaPV serum samples, which was comparable to the ID. Vet ELISA; the novel assay was also able to detect total CaPV antibodies earlier than the commercial kit (W. Wang *et al.*, 2025).

LSDV 034 also seems to be a suitable antigens for serology: a competitive ELISA based on LSDV034 showed sensitivity and specificity of 99.6% and 100% respectively, in serum samples from cattle either infected with LSDV or immunised with a live attenuated vaccine (LAV) based on GTPV (Yuan *et al.*, 2024b).

More recently, two studies also report promising advances towards an effective ELISA. Kumar *et al.* (2026), produced and used recombinant LSDV P32 and B5R antigens in an indirect ELISA to test geographically diverse known-positive serum samples, with encouraging results warranting further development of the assay (A. P. Kumar *et al.*, 2026). Alongside, researchers working in China have developed a competitive ELISA based on a novel monoclonal antibody targeting LSDV001, based on the recognition of this antigen in bovine immune sera; the assay performed with an overall sensitivity of 96.83% and specificity of 98.00% when tested on samples of bovine serum from cattle infected or vaccinated in the field or under laboratory conditions, and positive or negative by VNT (Li *et al.*, 2026).

While these studies, taken together, have suggested several possible diagnostic antigens that might be used to develop an improved ELISA for LSDV or CaPV, there is a lack of rigorous cross-testing under standardized conditions and so it remains unclear which antigens are optimal and should be focused on as leading candidates. A recent report by Teffera *et al.* (2026) aimed to fill this knowledge gap by comparing a set of proteins that were previously reported as potentially immunogenic surface-expressed proteins (LSDV 60 (L1R), LSDV 74 (p32), LSDV 117 (A27L), LSDV 122 (A33R), LSDV 123

(A34), and LSDV 141 (B5R)) in an indirect ELISA to detect anti-CaPV antibodies. For each susceptible species, the authors identified several antigens that had higher sensitivity than the ID Vet ELISA on test-sera: LSDV 122, 60 and 117 performed best for sera from goats; LSDV 122, 123 and 60 were best for sera from sheep; and LSDV 122 performed best for cattle (Teffera *et al.*, 2026). Overall, LSDV 122 had the highest sensitivity and specificity in ELISA across all CaPV-susceptible species tested (96% or higher) and was highlighted by the authors as a strong candidate for a single-antigen CaPV ELISA (Teffera *et al.*, 2026).

Of note, although the ID.Vet ELISA is validated for use with serum and plasma, minor modifications to the protocol may enable detection of LSDV antibodies in milk. Researchers found that in approximately 65% of confirmed cases, this non-invasive sampling method could be used successfully with the commercial kit (Milovanović *et al.*, 2020). While the lowered level sensitivity of this approach would currently limit widespread application, this study does highlight the potential for relatively minor modifications to existing protocols that could offer real advantages to livestock-keepers seeking to test large numbers of animals or to gather samples without the need of any specialist skill or equipment.

Immunoperoxidase monolayer assay

In 2020, Haegeman and colleagues reported the development of an immunoperoxidase monolayer assay, in which a cell monolayer is infected with LSDV and subsequently inactivated for use as the antigen. When evaluated against VNT and the ID.Vet ELISA, this assay demonstrated comparable specificity but much greater sensitivity, enabling detection of antibodies as early as 8 days post-infection and 10 days post-vaccination, whereas the comparator assays did not detect positive animals at these early time points (Haegeman *et al.*, 2020). Additional advantages include high sensitivity and specificity coupled with procedural simplicity, minimal equipment requirements, and the use of crude infected-cell antigen that can be fully inactivated in-plate and stored at −20 °C or −80 °C for at least 2 months without affecting performance. The authors noted, however, that while this method is well suited for early detection in small- to medium-scale testing, the ID.Vet ELISA is more practical for high-throughput applications (Haegeman *et al.*, 2020).

Luminex

Luminex technology uses magnetic polystyrene beads coated with different antigens to detect specific serum antibodies via flow cytometry. Berguido *et al.* (2024) developed and evaluated a Luminex-based serological assay capable of simultaneously detecting antibodies against LSDV ORF123 (conserved across LSDV, GTPV, and SPPV) and Rift Valley fever virus in cattle, sheep, and goats (Berguido *et al.*, 2024b). This approach demonstrated 99% sensitivity and 98% specificity for detecting anti-LSDV antibodies in cattle, and 100% sensitivity and specificity for detecting SPPV- and GTPV-specific antibodies in sheep and goat sera (Berguido *et al.*, 2024b).

Future studies could explore the use of the antigens described above in the ELISA section as reagents for application in Luminex assays.

Laser-induced graphene (LIG)-based electrochemical immunoassay

A group working in Thailand recently reported their work towards developing a field-deployable biosensor based on detection of F13L antigen (a conserved surface-exposed EEV protein) by immobilized IgM; the assay exhibited 95% sensitivity and 100% specificity using serum from vaccinated and naturally infected cattle (Suea-Ngam *et al.*, 2026). Notably, by immobilizing F13L the assay could be used instead to detect antibodies to LSDV as part of vaccine monitoring.

Machine learning

As well as interest in the use of machine learning to predict likely locations of LSD outbreaks based on geospatial and meteorological data (Afshari Safavi, 2022), the integration of machine learning, artificial intelligence, and biosensor data shows potential for automated identification of LSD-affected cattle.

Toward this aim, Alam *et al.* (2025) used Inception V3 to extract features from complex lesion patterns in 3,000 images of LSD-affected cattle from the Kaggle database (Banachewicz and Massaron, 2022), and then employed support vector machines to classify these features. This approach correctly distinguished LSDV-affected from healthy skin in 80% of cases, and accurately determined lesion severity in 84% of cases, representing a clear improvement over other machine learning models, including logistic regression, random forest, decision tree, and AdaBoost) (Alam *et al.*, 2025).

Using 125 images collected from local farms, an ensemble approach combining imaging and temperature sensor data achieved an accuracy of 86% in identifying LSDV-affected animals after training on 375 images from farms in Pakistan (Khaskheli *et al.*, 2025). Alkhanifer and AlZubi (2025) reported higher accuracy using approximately 2,000 images of LSD-affected and healthy cattle from Vechur, Swiss Holstein, Jersey, and Ponwar breeds to train a DenseNet-121 convolutional neural network (CNN). This model achieved an overall accuracy of 93% in distinguishing LSDV-affected from healthy cattle (Alkhanifer and AlZubi, 2025), and represents a successful improvement on the group's previous work using a similar CNN model, which achieved a lower accuracy of 87% (AlZubi, 2024), highlighting the importance of optimising model parameters before adopting such approaches.

As recently reviewed (Thiele *et al.*, 2023), CNN-based methods have several limitations, including high computational and data-labelling requirements, substantial memory consumption, and challenges in interpretation and application to sequential data. In addition, some models require long training times and relatively slow processing. To address these constraints, Saqib *et al.* (2024) applied a MobileNetV2 architecture with the RMSprop optimiser to analyse images of cattle and identify those affected by LSD. After training on 1,000 images of affected and unaffected cattle, the model achieved an average precision, sensitivity, F1-score, and accuracy of 95% (Muhammad Saqib *et al.*, 2024).

Given the growing interest in machine learning for LSD detection, comparative evaluations are important for understanding the advantages and disadvantages of different approaches. Senthilkumar *et al.* (2024) compared multiple models, including Xception, VGG16, VGG19, ResNet152V2, InceptionV3, MobileNetV2, DenseNet201, NASNetMobile, NASNetLarge, and EfficientNetV2S, using approximately 3,000 diverse publicly available images. VGG16 and MobileNetV2 showed the highest performance, with accuracies of 96%, sensitivities of 94% and 99%, and specificities of 97% and 95%, respectively (Senthilkumar *et al.*, 2024). Notably, most of these approaches are not yet readily applicable to grazing herds and may be difficult to implement in low-resource settings.

Perhaps the most promising advance in this field was reported in a study by Ulaah *et al.* (2025) that used 6000 images of cattle with or without LSD from the Kaggle database to train a model that exploited Vision Transformers to increase accuracy and precision. Overall, the model performed with 98% accuracy, 99% precision and 99% recall across 2000 test images of LSD-affected and -unaffected cows (Ullah *et al.*, 2025). A key aspect was the adaptation of the technology to be used via a smartphone application, rendering this preliminary diagnostic tool highly accessible to farmers in the field.

Overall, while machine-learning approaches might be considered a useful part of the toolkit for herd monitoring and have advanced significantly in recent years, they are not applicable to all settings and should be considered a supportive approach rather than a replacement for definitive laboratory diagnostics.

Differentiating infected from vaccinated animals (DIVA)

Several studies have reported important advances in DIVA over the past 10 years. This is particularly relevant for identifying active infections in newly vaccinated herds, where vaccine and field strains may co-circulate and either could be the cause of visible lesions, and for enabling trade with regions that use vaccination while maintaining disease-free status.

Genetic DIVA

Genetic DIVA is a term coined to describe the molecular assays that can distinguish vaccine versus field isolates of a pathogen based on differences in their genetic code. Complete genome sequencing can differentiate CaPV LAVs from virulent isolates, but is costly and time-consuming, rendering it an impractical approach to large-scale diagnosis or monitoring. To fill this unmet need, new molecular approaches have been developed based on defined genetic differences between vaccine and field strains of LSDV.

Several of these approaches based on real-time PCR assays are now commercially available, including the ID Gene™ LSD DIVA Triplex kit and the Bio-T kit® LSD—DIVA. However, these assays can be costly, and their primers, probes, and

reagents may not always be readily accessible. Moreover, while they perform well for European LSDV isolates and Neethling-based LAVs, they cannot distinguish vaccine-like recombinant viruses that have emerged since 2017 (Byadovskaya *et al.*, 2020).

As a result, alternative approaches using standard PCR reagents and protocols have been developed. In 2017, researchers in Greece developed and validated both a PCR–Restriction Fragment Length Polymorphism method targeting the LSDV127 gene (Agianniotaki *et al.*, 2017b) and a duplex quantitative real-time PCR assay targeting the GPCR gene (Agianniotaki *et al.*, 2017a) to enable DIVA for locally circulating field strains and LSDV LAVs. Next, Vidanović *et al.* (2021) developed two TaqMan PCR assays for wild-type strains (based on their earlier work (Vidanović *et al.*, 2016)) and Neethling-based LAV strains, achieving diagnostic sensitivity and specificity of at least 97% and 100%, respectively, compared to the Bowden CaPV real-time quantitative PCR (Vidanović *et al.*, 2021). Haegeman *et al.* (2023) also designed a real-time duplex PCR that was able to discriminate Asian field and recombinant vaccine strains from Neethling-based vaccines by targeting conserved regions of the DNA ligase-like (LD133) gene and the kelch-like protein (LD144) gene (Haegeman *et al.*, 2023b). Similarly, Agianniotaki *et al.* (2021) reported a multiplex real-time PCR targeting the EEV gene region intact in wild-type LSDV but deleted in Neethling-based LAVs, enabling reliable identification of infected or co-infected cattle compared with recently vaccinated animals (Agianniotaki *et al.*, 2021).

Other groups also report noteworthy progress. In 2021, Wolff *et al.* developed duplex qPCR assays capable of distinguishing all three CaPVs and differentiating LSDV vaccine and field strains, including in mixed samples (Wolff *et al.*, 2021a). More recently, Elsheikh *et al.* (2024) developed a conventional PCR-based DIVA method targeting the EEV gene which was applicable to DIVA with the MEVAC LSD vaccine but not to the Egyptian Al-Abbasya vaccine, which shares this genomic region with circulating field strains (Elsheikh *et al.*, 2024). This highlights the importance of considering strain differences and local conditions for the development of effective DIVA strategies.

Three papers describe the use of high-resolution melting qPCR for genetic DIVA of LSDV. Menasherow *et al.* (2016) described a modified high-resolution melting qPCR protocol for detecting a 27-base-pair fragment of the LSDV126 EEV gene present in field strains but absent from the Neethling vaccine strain (Menasherow *et al.*, 2016). Meanwhile, in India, Kumar *et al.* (2023) developed a high-resolution melting-based gap qPCR assay targeting the 801-nucleotide deletion in the 5’ inverted terminal repeat (ITR) region that distinguishes Lumpi-ProVacInd from both Neethling-based LAVs and local field strains, demonstrating near 100% sensitivity and specificity in laboratory testing with DNA-spiked samples, although field testing remains to be performed (R. Kumar *et al.*, 2023a). Successful DIVA has also been reported using multi-locus real-time PCR combined with HRM analysis targeting ORF095, ORF126, and ORF145, which differ between vaccine strains and dominant recombinant Asian field strains (Bhakha *et al.*, 2025).

Two other situations pose slightly different challenges: outbreaks following heterologous LAV use, and outbreaks that might be related to vaccine strains. India, for example, has historically used heterologous LAVs for LSDV prevention, necessitating the development of simple and cost-effective molecular tests for DIVA. In 2023, Nandi *et al.* identified a 27-nucleotide deletion in the LSDV126 gene (encoding the EEV protein) present in circulating LSDV isolates but absent in GTPV and vaccine strains, confirming earlier sequencing work (Erster *et al.*, 2019; Menasherow *et al.*, 2016). Based on this, they developed an isothermal polymerase spiral reaction assay suitable for pen-side testing, with high specificity and sensitivity comparable to real-time PCR (Nandi *et al.*, 2023). In the case of outbreaks involving recombinant LSDV strains, such as those linked to poorly controlled LAV use, the genetic similarity of the vaccine strain to field strains makes DIVA especially difficult. In response, Sprygin *et al.* (2019b) developed single-run real-time PCR assays to detect vaccine-derived field strains circulating in the Russian Federation and distinguish them from the Neethling vaccine strain, reporting high sensitivity and specificity compared to complete sequencing and virus isolation (though these data were not shown) (Sprygin *et al.*, 2019b).

Serological DIVA

Several serological approaches to DIVA have also been trialled, either to directly detect the virus present or to discriminate between the humoral response of animals to vaccine or field strains.

In the former category, Chang and colleagues (2025) developed a double-antibody sandwich ELISA to distinguish cattle recently immunised with GTPV LAV from those infected with LSDV. The researchers generated two murine monoclonal antibodies specific for LSDV P32 that did not cross-react with SPPV or GTPV (Chang *et al.*, 2025a). Although results were promising *in vitro*, the assay has not yet been validated using field samples.

More commonly, serological DIVA relates to the detection of antibodies formed by animals that are specific to antigens present on the in the case of vaccination or virulent infection. DIVA has been achieved using an indirect ELISA based on a B22R protein fragment present in major SPPV/GTPV vaccines and both Neethling-based and KSGP-0240 LSDV vaccines (Biswas *et al.*, 2019), but absent from field strains of LSDV, SPPV or GTPV. This approach demonstrated >99% sensitivity and specificity when tested using serum from animals infected with wild-type CaPVs (Berguido *et al.*, 2023), and offers advantages in terms of compatibility with existing vaccination strategies.

More recently, an ELISA-based DIVA approach for cattle vaccinated with Lumpi-ProVacInd or infected with local isolates was developed based on detection of antibodies to an ORF154-encoded protein, which is deleted in the vaccine strain (Nokhwal *et al.*, 2025).

Lastly, to enable DIVA in cattle vaccinated with a GTPV LAV versus those infected with LSDV, Yuan *et al.* (2024) synthesised a recombinant protein comprising six LSDV-specific sequences for use in an in-house indirect ELISA. This

approach achieved 100% diagnostic specificity and 93% diagnostic sensitivity across 200 serum samples (Yuan *et al.*, 2024a) and may represent an important step toward DIVA in regions using heterologous LAVs.

While these studies represent important first steps towards new serological DIVA diagnostics, there is a lack of consistent approach to validation and reporting, and all require further testing against a panel of fully characterized positive and negative serum samples, and comparison with VNT and established ELISAs to fully determine their actual sensitivity and specificity.

Sampling strategies and other developments

A 2025 study reported the first use of a cellular interferon (IFN)-γ-release assay for LSDV diagnosis. With the possible exception of the immunoperoxidase monolayer assay described by Haegeman *et al.* (Haegeman *et al.*, 2020), this approach was uniquely able to detect cell-mediated immunity to heat-inactivated antigen from as early as 10 days post-vaccination and 7 days post-infection in all animals, with specificity of up to 100% (Kresic *et al.*, 2025).

Detection of subclinical infection within affected herds remains challenging, as blood samples are not consistently positive for viral DNA in these animals. One study found that ear-notch or skin biopsy samples were consistently positive even in subclinical infection from day 16 post-infection, although blood remained the preferred sample type for confirming infection in cattle with clinical LSD (Aerts *et al.*, 2021). These findings are consistent with earlier work by the same group (Haegeman *et al.*, 2021a), but suggest higher rates of viral detection in skin samples from subclinical cases than previously reported (Sanz-Bernardo *et al.*, 2021). Identifying possible factors underlying these differences may provide broader insights into disease biology.

To improve recovery of live virus from dilute samples, such as those obtained from asymptomatic animals, Nanotrap® Microbiome A Particles show promise. One study demonstrated that their use increased the sensitivity of CaPV detection by subsequent PCR by up to 100-fold, and that captured viruses remained viable for isolation in lamb kidney cells (Das *et al.*, 2024).

Limited access to veterinary training in affected regions can hinder accurate diagnosis and management of animal diseases. One approach to address this is the use of mobile phone applications; a pilot study in Ethiopia showed that such tools could support veterinary students in generating differential diagnoses with associated probabilities based on observed clinical signs (Beyene *et al.*, 2017).

Emerging technologies for monitoring cattle health include wearable devices and biosensors (reviewed in (Alipio and Villena, 2023)). These technologies aim to capture parameters similar to those used in camera-based systems but are

better suited to grazing animals, enabling real-time monitoring of indicators such as body temperature, heart rate, and activity. A pilot study in Pakistan highlighted the potential of a low-cost wearable device to identify cattle showing early signs of illness, supporting earlier detection of LSDV infection (Shahab *et al.*, 2024).

In some settings, diagnostic capacity remains constrained by limited engagement with farmers and stakeholders, alongside challenges including lack of equipment, high reagent costs, and insufficient training of laboratory personnel, as reported in Uganda despite increased funding (Vudriko *et al.*, 2021).

Pathogenesis

The disease caused by LSDV is highly variable, ranging from subclinical to severe; this has been observed both in experimentally infected cattle and in the field (Babiuk *et al.*, 2008b). Host entry by LSDV occurs mainly via the skin, where the virus targets susceptible cell populations in the epidermis and dermis. This initial infection causes a histocytic inflammation with necrotising vasculitis in deep dermal blood vessels that results in the formation of nodular skin lesions ((Sanz-Bernardo *et al.*, 2020); reviewed in (N. Kumar *et al.*, 2025)). Following viral replication in the skin, LSDV spreads throughout the host, allowing further replication and spread. LSDV then enters the bloodstream, causing viraemia and infecting distal organs (reviewed in (N. Kumar *et al.*, 2025; Mulatu and Feyisa, 2018)). This viraemia has substantial systemic effects on the host, including alterations in blood cell counts, metabolism, oxidative stress, and circulating levels of many multifunctional factors such as cytokines, cortisol, liver transaminases, bilirubin, and glucose. Numerous studies have characterised these cytological and biochemical changes associated with LSDV infection (Abutarbush, 2015; El-Mandrawy and Alam, 2018; Kamr *et al.*, 2022; Roy *et al.*, 2025; Salama *et al.*, 2024; Saleh *et al.*, 2023; Sandeep *et al.*, 2023a; Şevik *et al.*, 2016; Tran *et al.*, 2023; Ul-Rahman *et al.*, 2023), and serum IL-6 has been proposed as a biomarker for predicting disease progression in cattle (W. Ahmad *et al.*, 2023b). Although mortality is generally low, it can be higher in certain virus strain–host breed combinations. For example, experimental infection with a Nigerian strain (LSDV-V/281-Nigeria, originally isolated from an LSDV-positive cattle skin sample in 2018) induced severe disease and approximately 33% mortality in naïve Holstein Friesian cattle (Wolff *et al.*, 2021b). Similarly, infection of indigenous cattle in Kazakhstan with the local isolate KZ-Kostanay-2018 resulted in a clinical profile comparable to the Russian Saratov/2017 strain, but with more rapid onset and greater severity (Kutumbetov *et al.*, 2025).

LSD is also associated with immunosuppressive effects in affected animals (Neamat-Allah, 2015), and frequently co-occurs with other ruminant diseases, including theileriosis, babesiosis, and anaplasmosis (Abas *et al.*, 2021; Reddy *et al.*, 2025a; Sumbria *et al.*, 2026; Zaitoun *et al.*, 2022). Numerous bacterial species, including multidrug-resistant strains, have been isolated from LSDV-infected cattle (Abdel Kawy *et al.*, 2021). Omoniwa *et al.* reported the first case of co-infection

with LSDV and pseudocowpox virus, a *Parapoxvirus* with similar clinical features that is often misdiagnosed in field settings (Omoniwa *et al.*, 2023).

***In vivo* studies**

Mishra *et al.* compared the genomes of LSDV isolates from the 2019 and 2022 outbreak waves in India (discussed in more detail below), with the latter associated with substantially higher virulence (Mishra *et al.*, 2024). The researchers identified numerous genetic differences, highlighting in particular a 12-nucleotide deletion in the viral GPCR gene and a 95-nucleotide deletion in the functional resolution sequence (Mathijs *et al.*, 2022) of the 2022 isolate (Mishra *et al.*, 2024).

In a study of LSDV strains circulating in Russia (also discussed below), Shumilova *et al.* compared pathology associated with three isolates—the classical cluster 1.2 strain Dagestan/2015 and the recombinant vaccine-like cluster 2.1 and 2.2 strains Saratov/2017 and Udmurtiya/2019, respectively. Overall gross pathology was similar across strains, although lymph node-specific pathology was observed only with the Dagestan/2015 and Udmurtiya/2019 strains (Shumilova *et al.*, 2023).

Truong and Tran *et al.* performed RNA sequencing of small non-coding RNAs isolated from serum-derived exosomes in LSDV-infected cattle, with a focus on piwi-interacting RNAs (piRNAs) (Truong *et al.*, 2025b). Among more than 17,000 differentially expressed non-coding RNAs identified in exosomes from infected versus control serum, 80 piRNAs were upregulated and 346 were downregulated (Truong *et al.*, 2025b).

***In vitro* studies**

Although the clinical presentation of LSD in cattle is well characterised, the determinants of strain-specific virulence remain less clear. *In vitro* studies provide controlled systems for examining links between viral genetic variation and pathogenesis.

Recombination events can influence LSDV pathogenesis. A comparison of the classical Russian field isolate Dagestan/2015 with the recombinant vaccine-like strain Saratov/2017 (discussed below in Epidemiology) showed that the latter replicated more rapidly and exhibited more aggressive growth in primary lamb kidney and testis cells; this observation was supported by *in vivo* skin inoculation experiments (Kononova *et al.*, 2021). Although differences in morbidity and mortality have not been observed between the recombinant and classical field viruses in the field, the widespread use of live attenuated LSDV vaccines (discussed below) has raised concerns regarding reversion to virulence (Biswas *et al.*, 2019). Van Schalkwyk *et al.* analysed virulent vaccine-associated subgroup 1.1 LSDV isolates collected in

South Africa between 1991 and 1997, comparing them LAV strains (also subgroup 1.1) and virulent wild-type strains (subgroup 1.2) (Schalkwyk *et al.*, 2020). They identified 67 single nucleotide polymorphisms distinguishing vaccine and vaccine-like strains, 40 of which were shared with wild-type strains, suggesting selection-driven genetic drift toward increased virulence (Schalkwyk *et al.*, 2020). Similarly, Erster *et al.* reported that virulence in Israeli isolates was associated with duplication of a 27-bp region in the LSDV126 gene when compared with Neethling vaccine strains (Erster *et al.*, 2019).

LSDV infection seems to induce apoptosis and activate the unfolded protein response *in vitro* through endoplasmic reticulum stress, although this response appears to be detrimental to viral replication and its precise role remains unclear (Tan *et al.*, 2023b, 2023a). Ren *et al.* further reported activation of the DNA damage response in infected cells, promoting viral replication via the ATM–Chk2 signalling pathway (Ren *et al.*, 2025).

LSDV may also exploit peripheral blood mononuclear cells (PBMCs) for dissemination within the host. Kumar *et al.* generated recombinant LSDV expressing green fluorescent protein (GFP) and used it to infect bovine PBMCs, finding that although the virus did not replicate in these cells, it suppressed antiviral responses and could be transmitted to other permissive cells in co-culture (M. Kumar *et al.*, 2025) (see Immune Evasion below).

Finally, microRNA (miRNA) profiling of LSDV-infected primary lamb testis cells identified widespread disruption of miRNA expression during infection, affecting multiple cellular pathways, including calcium reabsorption, aldosterone synthesis and secretion, and melanogenesis (Pandita *et al.*, 2023).

Immunology

Cattle that survive infection with LSDV are generally considered to develop lifelong immunity (Weiss, 1968), yet the mechanisms underlying this durable protective response remain incompletely defined. Both cell-mediated and humoral immunity are known to play important roles, but a more detailed understanding of the key antigens, pathways, and cellular components involved is still lacking. Such insight would support the rational design of improved vaccines and therapeutics.

Immunogenetics

It has long been recognised that European cattle breeds (*Bos taurus*) are typically more susceptible to severe clinical LSD than indigenous African and Asian breeds (*Bos indicus*), although the mechanisms underlying this difference remain unclear. A recent transcriptomic study compared resistant and symptomatic individuals within a cohort of Holstein cattle, finding that lower baseline expression of the Interleukin 1 Receptor Accessory Protein was associated with resistance,

alongside differential regulation of a set of immune-related genes at day seven post-infection (Hossein Banabazi *et al.*, 2025). Another study putatively identified levels of expression of miR-29a as a possible factor contributing to the differential susceptibility of native Indian and cross-bred cattle to LSDV (Kumar *et al.*, 2024). Together, these findings warrant further investigation, including comparisons across a range of breeds.

Inter-breed differences may also occur in response to the Neethling LAV. One study reported significantly lower seroconversion in Hanwoo and Jersey cattle compared with Holsteins, with differences emerging from 6 weeks post-vaccination and correlating with variation in pre-vaccination immune cell profiles (Bok *et al.*, 2025). If confirmed, these observations may have implications for vaccine testing and deployment in the field.

Innate immunity

Relatively few studies have examined interactions between LSDV and the host innate immune response.

In one study, a small cohort of cattle was intravenously inoculated with an LSDV field strain, and serum-derived exosomes were analysed for miRNA content. Approximately 1,000 miRNA transcripts were identified (Truong *et al.*, 2025a). Compared with controls, sera from LSDV-infected cattle contained significantly more miRNAs targeting genes involved in immune responses, signalling pathways, and virus–host interactions. The researchers highlighted the miRNA let-7 family as a candidate for further study, based on its known role in hepatitis C virus infection (Chen *et al.*, 2019).

Adaptive immunity

Much about the immune response to natural infection with LSDV remains unknown, though many studies report the response to novel and established vaccines (see Vaccines section); however, as these vaccines are attenuated, there will necessarily be differences. A single study was published in 2022 which aimed to fill this critical knowledge gap (P. C. Fay *et al.*, 2022), but was later retracted. Here, we report on the few studies that have characterised cytokine profiles and oxidative stress responses associated with the later stages of LSDV infection and therefore deemed relevant to adaptive immunity.

In 2023, Sandeep *et al.* studied 24 naturally infected cattle and reported elevated serum levels of IgG and IgM, as well as IL-4, TNF-α, and IFN-γ; cattle also exhibited increased markers of oxidative stress, compared with healthy controls (Sandeep *et al.*, 2023b). The authors did not address the cellular immune response. In a more recent study of 20 infected cattle, researchers similarly reported elevated oxidative stress markers and increased levels of TNF-α, IL-10, IFN-γ, and IL-6, which remained higher than in controls over a 4-week period. The researchers suggested that viral infection may also induce cardiac and/or hepatic stress responses (Mahajan *et al.*, 2025). These findings align with earlier work in Egypt,

where naturally infected cattle showed increased liver enzyme levels and elevated TNF-α and IL-4 (Yanni *et al.*, 2021), as well as with a study in Vrindavani cattle in India, which reported higher levels of liver enzymes, IL-4, and IL-10 in infected animals, alongside relatively lower levels of IL-2, granulocyte-macrophage colony-stimulating factor (GM-CSF), and IL-6 (S. F. Ahmad *et al.*, 2023).

A study of a vaccine-related recombinant LSDV strain circulating in Thailand in 2021 found that PBMC transcript levels of IFN-γ and TNF-α were higher in infected cattle than in healthy animals, whereas IL-10 levels were lower (Suwankitwat *et al.*, 2023a). Two additional observations from this study are notable. First, farms implementing external parasite control programmes had approximately half the LSD-related morbidity rates. Second, antibody titre correlated positively with disease severity, whereas IFN-γ levels at symptom onset showed a negative correlation, including in animals with subclinical or mild disease that were subsequently protected from reinfection for at least 15 months (Suwankitwat *et al.*, 2023a). If confirmed in a natural infection with a fully virulent strain, these findings may have implications for understanding the relationship between adaptive immunity and disease severity, and for vaccine development.

A single study examined early skin lesions of LSDV-affected cattle and identified IFN-γ-producing cells, $CD4^+$ T-cells and macrophages as key players in the local immune response, and perhaps also as mediators of immune pathology in lesion-affected skin (Badr *et al.*, 2022). This study provides a good starting point for future, more detailed studies of the local immune response to infection.

Immune evasion

Many studies have explored the potential immune-evasive functions of LSDV proteins.

Because LSDV replicates its DNA in the cytoplasm, its genome would be expected to be detected by the cytosolic pattern recognition receptor cGAS (cyclic GMP–AMP synthase), triggering downstream signalling via STING (stimulator of interferon genes, also known as MITA) and activation of interferon regulatory factor (IRF) 3 (Sun *et al.*, 2013). IRF3 activation can, in turn, promote the transcription of antiviral effectors, including type I interferons (IFNs). Viral proteins that interact with this pathway could therefore have substantial effects on host innate immunity.

Li *et al.* (2025) showed that LSDV087 not only has a host mRNA-decapping function, but also interacts with STING, promoting its polymerisation and inhibiting its degradation in HEK-293 cells, leading to increased activation of the IFN-β promoter (Z.-Z. Li *et al.*, 2025). Using a murine cell line stably expressing LSDV087, the researchers further demonstrated enhanced activation of TNF–NFκB pathways in response to exogenous dsDNA (Z.-Z. Li *et al.*, 2025). These findings were confirmed in MDBK cells, although it remains unclear whether the same mechanisms operate *in vivo* or how LSDV087 influences disease pathogenesis.

TANK-binding kinase 1 (TBK1) is a key mediator linking pathogen sensing to transcription of innate immune effectors (Fitzgerald *et al.*, 2003). In 2022, Yang *et al.* cloned full-length TBK1 from cows and goats and confirmed its role in IFN-β induction *in vitro* (Yang *et al.*, 2022). More recently, Liang *et al.* (2024) showed that LSDV suppresses expression of IFN-β and interferon-stimulated genes (ISGs) in MDBK cells, with a substantial contribution from ORF127 (Liang *et al.*, 2024). The researchers demonstrated that ORF127 inhibits ubiquitination of TBK1, a step required for its phosphorylation and downstream activation of IRG3 (Tu *et al.*, 2013).

Wang *et al.* (2025) reported that several LSDV proteins inhibit IRF3 activation and suppress IFN-β transcription in MDBK cells (J. Wang *et al.*, 2025). Focusing on ORF142, they showed that this protein promotes lysosomal autophagic degradation of STING, suggesting a mechanism of immune evasion. These findings align with work by Chen *et al.* (2025), who showed that ORF142 inhibits IFN-β transcription in HEK-293T cells by preventing nuclear translocation of IRF3 through disruption of its interaction with TBK1 (Z. Chen *et al.*, 2025). Similarly, the ORF137 protein inhibits phosphorylation of IRF3 *in vitro*, reducing transcription of IFNs and ISGs in HEK-293T cells (Ke *et al.*, 2025).

Li *et al.* (2025) investigated ORF151, showing that overexpression of this protein in HEK-293T cells reduced IFN-β mRNA levels following herpes simplex virus infection. Deletion of ORF151 in recombinant LSDV resulted in reduced viral replication and increased expression of host genes encoding IFN-β, IL-6, and NFκB-1, as well as apoptosis-associated genes, in MDBK cells (J. Li *et al.*, 2025). The researchers proposed that this mutant virus might represent a candidate LAV, although this was not tested *in vivo*.

Another mechanism of IFN modulation involves LSDV012, one of the ankyrin repeat proteins (Tulman *et al.*, 2001). This protein strongly antagonises interferon-induced protein with tetratricopeptide repeats 1 (IFIT1), leading to reduced transcription of IFN-α/β in several mammalian cell lines (Xie *et al.*, 2025). A recombinant virus lacking LSDV012 produced significantly smaller lesions in mice compared with the wild-type virus. Notably, orthologues of this protein in GTPV and SPPV (GTPV_gp010 and SPPV_010) bind bovine IFIT1 but not human or bat IFIT1, suggesting a degree of species-specificity (Xie *et al.*, 2025). The researchers speculated that this observation could be an important part of the broader mechanisms determining susceptible species for these pathogens (as reviewed in (Rothenburg and Brennan, 2020)).

In addition to suppressing IFN induction, LSDV can inhibit downstream signalling. Sun *et al.* (2026) showed that LSDV122 interacts with subunits of the type I IFN receptor, preventing downstream kinase signalling and thereby inhibiting ISG transcription (Sun *et al.*, 2026). A recombinant virus lacking LSDV122 induced higher levels of IFN-β *in* MDBK cells and was more immunostimulatory *in* mice (Sun *et al.*, 2026).

LSDV001/156 is a late-expressed gene product encoded within the ITR region that contributes to viral replication and is incorporated into virions (Schlosser-Perrin *et al.*, 2023). Recent work suggests an additional role in immune evasion. Zhang *et al.* (2025) showed that deletion of LSDV001/156 in MDBK cells led to increased activation of IRF3-dependent pathways, and a parallel *in vivo* study in cattle reported reduced virulence and pathogenesis of viruses lacking this gene (M. Zhang *et al.*, 2025). The researchers speculated that these effects were due to the absence of its IFN-reducing role. However, given the protein's functions in viral replication, it is challenging to distinguish the relative contribution of its different properties to virulence *in vivo* during a natural infection.

Beyond IFN-related pathways, LSDV also seems to modulate host cell autophagy. Autophagy contributes to innate defence through lysosomal degradation of intracellular pathogens and antigen presentation (recently reviewed in (Xie *et al.*, 2026)). Tan *et al.* showed that LSDV induces autophagy and endoplasmic reticulum stress in bovine embryonic fibroblasts *in vitro* (Tan *et al.*, 2023a). Subsequent work by Sugunan *et al.* indicated that LSDV inhibits lysosomal degradation in MDBK cells while maintaining aspects of autophagy that support viral replication (Sugunan *et al.*, 2025).

Further evidence of immune modulation comes from studies in primary bovine PBMCs, where infection with a low-passage field isolate suppressed expression of ISGs during LSDV (M. Kumar *et al.*, 2025). Although LSDV was present in around 25% of the adherent PBMCs (after incubation at MOI 3 for 48 hours), it was unable to productively replicate. Despite this, infected PBMCs transmitted the virus to MDBK cells in direct co-culture, leading to infection of the cell line (M. Kumar *et al.*, 2025). The mechanism underlying this apparent cell–cell transmission was unclear, but the researchers identified three possibilities: surface-bounce LSDV was transferred to the MDBK cells, LSDV was transferred after having entered PBMCs, and/or replicative naked viral genomes crossed over to cause infection. Whether PBMCs serve as disseminators of LSDV *in vivo* remains to be determined.

Supporting the relevance of these findings, Sun *et al.* reported minimal activation of type I IFN pathways in lesional and adjacent non-lesional skin from experimentally infected cattle (Sun *et al.*, 2026). It is yet unclear which of the inhibitory mechanisms identified *in vitro* operate in natural infection, but these observations represent an important step toward clarifying immune evasion *in vivo*.

Control of the disease

Vaccination is the most important control measure for LSDV. Following an LSD outbreak, no country has been able to eradicate LSDV using stamping out: only vaccination together with additional control measures is able to eradicate LSDV and allow the country to regain freedom from the disease, as first illustrated in Europe with the first LSDV outbreaks in Greece and the Balkans (reviewed in (Toker *et al.*, 2026)). It is important to note that an LSDV outbreak will require a much longer time to control and regain freedom compared to diseases that can be stamped out. This is also demonstrated by the situation in Europe, where recent FMD outbreaks were identified and controlled within a timeframe of months compared to the LSD outbreaks that are still not completely controlled.

Computational modelling

As LSDV continues to spread across three continents, biosecurity increasingly relies on evolving strategies that include risk prediction and management, regulation of animal movement, and development of effective countermeasures. Computational and mathematical modelling are becoming increasingly important in LSD epidemiology, particularly for identifying spatiotemporal disease clusters, estimating major risk factors, and predicting future transmission patterns (Demisie *et al.*, 2025; Renu and Yadav, 2025). Stochastic and probabilistic modelling approaches have also been used to estimate LSD-associated economic losses by incorporating variables such as direct mortality, reduced milk production, loss of draught power, and the costs of treatment and insect vector management (Naidu *et al.*, 2025).

Lee *et al.* conducted a systematic review of epidemiological modelling studies relating to LSD, focusing on key questions arising after outbreaks (e.g., outbreak origin, severity, and likely entry pathway) and the ability of different analytical modelling approaches to address these questions (Lee *et al.*, 2024). Based on these findings, the researchers proposed a structured modelling workflow to guide outbreak response and aid disease control decision-making. Importantly, they noted that their proposed workflow would be easier to implement in resource-rich settings than in resource-limited regions, where shortages of personnel and funding may force authorities to rely primarily on preventive measures without the support of pre-outbreak modelling (Lee *et al.*, 2024).

Machine learning techniques have also shown promise for predicting LSD outbreaks. An artificial neural network incorporating geospatial and meteorological variables achieved prediction accuracies of up to 97% against test datasets (Afshari Safavi, 2022). Ardestani & Mokhtari reported similarly promising results using a MaxEnt ecological niche model to estimate LSD risk in western Iran, where precipitation during the coldest season, isothermality, and average temperature during the wettest season contributed most strongly to modelled risk (Ardestani and Mokhtari, 2020). Khan *et al.* recently compared the autoregressive integrated moving average time series model against machine learning models for LSDV threat analysis in ten high-risk countries (Albania, Bulgaria, Greece, Israel, Malaysia, North Macedonia,

Russia, Serbia, Thailand, and Turkey), reporting lower prediction errors from support vector regression and decision tree models compared to the time series model (Khan *et al.*, 2026).

The rapid spread of LSD across neighbouring countries and trading partners in Southeast Asia and Europe has also prompted extensive biosecurity planning in Australia, where surveillance sensitivity has been reported at high levels (Mackereth *et al.*, 2024). Hall *et al.* evaluated the risk of LSDV introduction into Australia through long-distance windborne movement of insect vectors, assuming endemic disease circulation in Southeast Asia and Papua New Guinea (Hall *et al.*, 2023). Overall risk through this route was estimated to be very low, corresponding to approximately one predicted outbreak every 403 years. Importantly, however, this calculation rests on insect-to-bovine transmission requiring bites from 3–5 insects; the predicted risk could change in either direction as ongoing research continues to clarify the infectivity level of single LSDV-carrying insects (Hall *et al.*, 2023). A recent modelling study from Owada *et al.* corroborated the overall low risk of LSDV-carrying vector introduction in Australia, though areas in Far North Queensland and Port Hedland were identified as relatively more suitable for such an event compared to the rest of the country (Owada *et al.*, 2026). Another important limitation is that most studies examining LSDV risk in currently disease-free countries focus primarily on routes of introduction, leaving the potential transmission patterns of LSDV within these countries unexplored (Owada *et al.*, 2024).

LSD control can be especially difficult to achieve in economically disadvantaged LMICs, where agriculture often represents a key component of subsistence and may contribute approximately 15–30% of gross domestic product (Nuvey *et al.*, 2022). Regional sociocultural and religious factors may also influence disease control efforts. In India, for example, which contains nearly one-third of the world's cattle population, cows are regarded as sacred by adherents of several major religions, and slaughter is prohibited in most states (Datten *et al.*, 2023; Mathkari, 2025).

Vaccination campaigns may additionally be affected by local cultural (discussed below) and economic factors. In sub-Saharan Africa, where agriculture provides employment for more than 50% of the workforce (OECD and FAO, 2016), vaccination against LSD generally produces a positive return on investment. However, effective disease control will likely require integration of vaccination programmes with robust surveillance systems and vaccine delivery strategies capable of minimising poor field handling and cold-chain failures (Mwacalimba *et al.*, 2025; Nuvey *et al.*, 2022).

The development of rapid risk assessment models for potential disease introduction routes, including legal and illegal animal trade and movement of animal products, may help guide policy decisions and biosecurity measures (De Vos *et al.*, 2022). However, development of these models depends heavily on high-quality surveillance and disease reporting data that may not be available for LMICs (Roger *et al.*, 2017). A recent systematic review and meta-analysis of livestock biosecurity practices in Africa identified only 16 eligible studies from 1,408 screened records; these studies covered only

five countries (Egypt, Ethiopia, Nigeria, Tunisia, and Uganda), leaving more than 90% of the continent comparatively understudied (Ngom *et al.*, 2024).

In Southeast Asia, a range of factors have been associated with ineffective LSD control, including limited vaccine availability, inadequate surveillance infrastructure, illegal animal trade, wet markets that facilitate disease spread, and the environmental effects of climate change (Moudgil *et al.*, 2024; Windsor, 2024). International disease surveillance efforts are also complicated by geopolitical instability, which can leave regions less prepared for disease prevention, response, and control (reviewed in (Gongal *et al.*, 2022)).

Anthropogenic factors

Van Borm *et al.* recently conducted a comprehensive study of LSDV dispersal history and haplotype network analysis based on 72 viral genomes (Van Borm *et al.*, 2023). Among other findings, the researchers suggested that anthropogenic factors (primarily the generation of recombinants in the Lumpivax vaccine) likely underpinned the release of KSGP vaccine-like strains in East Africa and India, rather than endemic circulation of wild-type viruses in East Africa followed by introduction into India (Van Borm *et al.*, 2023; Vandenbussche *et al.*, 2022). Alongside vaccine production and trade-related animal movement, other important anthropogenic risk factors for LSD transmission include the presence of animal markets, co-grazing between herds, poor farm waste management, and inadequate on-farm vector control measures (Almuallem and Chauhan, 2025; Hässig *et al.*, 2015; Ince and Türk, 2020; Susanti *et al.*, 2023). Meanwhile, epidemiological modelling studies also frequently identify intra- and inter-country LSD clusters, underscoring the need for prevention and control strategies that account for both national and international transmission pathways (Punyapornwithaya *et al.*, 2025).

Strained diplomacy and ongoing geopolitical conflicts can seriously threaten the international cooperation required for effective disease monitoring and control (Tuppurainen *et al.*, 2020). Policies aimed at controlling transboundary diseases cannot be meaningfully evaluated without considering the impacts of conflict, which consistently disrupt animal welfare systems, livestock production, and disease surveillance and prevention infrastructure. The onset of the Syrian civil war in 2011, for example, was associated with marked increases in the prevalence of human and animal vector-borne diseases, including LSD, both within Syria and in neighbouring countries. These effects were linked to a breakdown in water and sanitation infrastructure, severe overcrowding, and reduced access to healthcare services (Albayrak *et al.*, 2018; Tarnas *et al.*, 2021).

Closely linked to effective disease control is the growing field of participatory epidemiology, which places greater emphasis on the experiences and priorities of livestock farmers and animal handlers, groups that are often underrepresented in discussions of biosecurity (Mulugeta *et al.*, 2025; Robi *et al.*, 2024a). Reduced LSD mortality has

been associated with several socioeconomic factors, including farmers' education and experience, household income, and access to information (Saqib *et al.*, 2023). Engagement with local socioeconomic and cultural contexts is therefore a critical step in translating disease control strategies into effective field implementation, reflecting the increasing recognition that "control measures, performing well in models or in theory, [are] useless without the support of relevant stakeholders" (Sauter-Louis *et al.*, 2021). Farmers' understanding of LSD directly influences management practices (Khan *et al.*, 2025; Sama *et al.*, 2026), suggesting that targeted education and training programmes could improve disease control outcomes. Participatory epidemiology studies can highlight specific local needs to which limited resources could be targeted to have the greatest impact (Duguma, 2020; Gambo *et al.*, 2018; Gizaw *et al.*, 2020), as well as specific misconceptions or traditional practices that could be addressed through veterinary outreach and future participatory initiatives (Gizaw *et al.*, 2020; Mburu *et al.*, 2023; Moje *et al.*, 2024; Sadia *et al.*, 2025).

In Bangladesh, a study of a 2019 outbreak in Barishal reported that only 20% of affected animals were treated by authorised veterinarians, whereas nearly 90% received non-steroidal anti-inflammatory drugs, followed by antibiotics, antihistamines, steroids, and/or antivirals (Khalil *et al.*, 2021). Similar challenges have been reported in Ethiopia, where limited investment in veterinary services and infrastructure has forced many veterinarians to rely heavily on personal experience and locally acquired knowledge for disease diagnosis and treatment, creating gaps in disease reporting and biosecurity that could potentially be reduced through improved training and access to animal health information networks (Makoga *et al.*, 2023; Nyokabi *et al.*, 2024).

Many Ethiopian farmers also rely partially or entirely on ethnoveterinary herbal medicine, which may represent a valuable source of potential therapeutics but is itself threatened by anthropogenic pressures such as deforestation (Hankiso *et al.*, 2024). Similar ethnoveterinary practices have also been documented among livestock farmers in Zambia (Syakalima *et al.*, 2018) and South Africa (Chakale *et al.*, 2022). A recent study from southwest Ethiopia found that only approximately 31% of surveyed farmers regularly used veterinary vaccines, attributable to deficits in disease knowledge, vaccine costs, and practical difficulties associated with administration (Robi *et al.*, 2024b).

Social pressure, perceived economic costs, and the opinions of local veterinarians can also strongly influence vaccination decisions during voluntary vaccination programmes (Mdlulwa *et al.*, 2019; Morgenstern *et al.*, 2024). In Israel, vaccination uptake among a cohort of 566 surveyed farmers declined from 61% in 2016 to 27% in 2019 (Morgenstern *et al.*, 2022). Notably, around half of the farmers who initially intended to vaccinate ultimately chose not to do so, primarily because of concerns regarding manpower requirements and vaccine cost, in what the researchers described as a "perception of low social pressure and lack of capacity" (Morgenstern *et al.*, 2022).

Therapeutics

Recombinant LSDV strains incorporating fluorescent and/or luminescent reporter proteins can facilitate faster screening of potential antiviral compounds via straightforward measurement of viral replication rates *in vitro*. For instance, Wang *et al.* used a partial thymidine kinase gene from pseudorabies virus as a homologous recombination sequence for insertion of the eGFP gene into LSDV (J. Wang *et al.*, 2024a). The researchers used this LSDV-ΔTK/EGFP recombinant strain to test 100 antiviral drugs *in vitro*, reporting that the polyphenolic phytochemical theaflavin had a strong antiviral effect, possibly via inhibition of viral entry into cells and subsequent replication(J. Wang *et al.*, 2024a). More recently, Gong *et al.* used CRISPR-Cas9 to insert two reporter genes (mCherry and firefly luciferase) between the viral ORF50 and ORF51 and, in line with previous findings (van Diepen *et al.*, 2021) reported that the resulting recombinant was phenotypically identical to the parental strain (Gong *et al.*, 2026). Use of this recombinant reporter virus for *in vitro* viral replication assays in MDBK cells identified six candidate antiviral drugs with inhibitory effects on viral and host nucleic acid synthesis, of which cytarabine demonstrated the greatest inhibition of viral replication relative to its minimal effects on host cells (Gong *et al.*, 2026).

Ibrutinib, a selective Bruton's tyrosine kinase inhibitor, demonstrated strong anti-LSDV activity via inhibition of viral DNA replication and protein synthesis in MDBK cells (Niu *et al.*, 2025). The class IIa histone deacetylase inhibitor TMP269 also inhibited LSDV replication in these cells (Cheng *et al.*, 2025). The researchers linked this activity to suppression of LSDV-promoted host lysophosphatidic acid metabolism and activation of the immunosuppressive MEK/ERK signalling pathway; this interpretation was supported by their demonstration that the lysophosphatidic acid receptor inhibitor Ki16425 also inhibited viral replication (Cheng *et al.*, 2025). In their recent study of the effects of LSDV infection on host kinase signalling pathways, Ren *et al.* reported that treatment of experimentally infected cows with an ATM kinase inhibitor reduced clinical symptoms (Ren *et al.*, 2025). Finally, *in vivo*, a five-day course of selenium and vitamin E treatment was reported to reduce LSD-induced oxidative stress and genotoxicity in cattle (W. Ahmad *et al.*, 2023a).

Although primarily focused on inhibition of African swine fever virus (ASFV) infection, Qian *et al.* reported that the alkaloid tetrandrine also exhibited antiviral activity against LSDV *in vitro* (Qian *et al.*, 2024). It remains unclear whether this activity is attributable to the same PI3K/Akt pathway inhibition underlying tetrandrine's anti-ASFV effects (Qian *et al.*, 2024). Zinc oxide nanoparticles also inhibited LSDV replication *in vitro*, although the 50% inhibitory concentration (45 µg/mL) exceeded the half-maximal cytotoxic concentration (31 µg/mL) in MDBK cells (El-Bagoury *et al.*, 2024).

As knowledge of the LSDV proteome continues to expand, computational modelling and bioinformatics approaches are increasingly enabling *in silico* screening of potential antivirals by predicting the strength and stability of interactions between molecules and viral proteins, thereby facilitating subsequent *in vitro* and *in vivo* studies. Krishna *et al.* conducted *in silico* ADMET (absorption, distribution, metabolism, and excretion) analysis alongside molecular docking and dynamics

simulations to evaluate 13 potential antiviral compounds against LSDV, reporting that the phytochemical derivative apigenin-4'-glucoside exhibited particularly strong predicted antiviral activity through interactions with several viral proteins, including the viral DNA and RNA polymerases (Krishna *et al.*, 2024). The honeybee peptide melittin was also identified as a potential inhibitor of CaPV RNA polymerase in a separate *in silico* study (Mustafa *et al.*, 2023). Zia & Sumon *et al.* identified four possible inhibitors of LSDV DNA polymerase, comprising two phytochemicals (rhein and taxifolin) and two FDA-approved antivirals (canagliflozin and tepotinib) (Zia *et al.*, 2024).

Vaccines

LAVs against LSD based on the Neethling strain have been available for decades, yet the disease remains a serious and growing threat. The original Neethling vaccine strain was attenuated from a field strain through repeated passage on primary lamb kidney cells and the chorioallantoic membranes of embryonated hens' eggs, and is currently produced by various companies globally, including Onderstepoort Biological Products (OBP) and Deltamune, the latter of which produces a slightly different variant marketed as Herbivac (highlighted here due to their prevalence in the vaccine studies reported below). Alongside these commercially available vaccines, locally produced LAVs offer the potential advantages of reduced cost, although some have demonstrated limitations in safety and efficacy where testing or production standards are insufficient.

While homologous LAVs may be effective, they are also associated with a set of side effects termed the "Neethling response" that varies in frequency and severity. This, combined with the sometimes difficultly accessing an affordable effective LAV led some countries have instead adopted heterologous LAVs based on SPPV or GTPV. However, these vaccines have shown variable success, and the search for improved alternatives continues. Considerable research has therefore focused on the development and testing of alternative vaccine platforms against LSD, including inactivated, multi-epitope, and multivalent approaches (discussed below).

Homologous LAVs

There is little doubt that well-produced and rigorously tested live attenuated LSDV vaccines can induce highly effective short- to medium-term protective immunity (reviewed most recently in (Maneekesorn *et al.*, 2025)). However, even the most effective homologous LSDV vaccines currently produce serological responses that are indistinguishable using currently available/validate tests from those generated by natural infection, some have undesirable side-effect profiles, and the immunological basis for strong versus weak protection seen in different settings remains uncharacterised.

Licensed homologous LAVs

The effectiveness of commercial Neethling-derived vaccines is well established and was recently convincingly evidenced by the vaccine-supported eradication of LSDV in Eastern Europe (European Food Safety Authority (EFSA) *et al.*, 2020). Due to the ever-changing disease landscape, continued assessment of their performance during outbreaks remains important, as does the characterisation of correlates of protection and the protective antigens involved.

During the 2015–2016 outbreaks across the Balkans, the vaccine was used widely and demonstrated a national effectiveness range of 63–97% (average 80%), with protective immunity developing approximately 2 weeks post-vaccination. The researchers proposed several possible explanations for this variation, including uneven geographical vaccine distribution, differences in the timing of viral exposure post-vaccination, and variability in reporting between countries (Klement *et al.*, 2020).

Concerns regarding the emergence of novel strains and their potential links to vaccine viruses have prompted studies of established vaccine efficacy in the face of new threats. For example, Philips *et al.* showed that three established Neethling-based LSDV vaccines were not only effective against clade 1.1 and 1.2 LSDV strains, but also performed strongly in cattle challenged with a virulent clade 2.5 recombinant strain (Philips *et al.*, 2024) that emerged following the release of vaccine-related strains in Russia in 2017 (Kononov *et al.*, 2019a). These findings are consistent with those from another 2024 study by Shumilova *et al.* (Shumilova *et al.*, 2024b).

There are also several studies presenting complete genome sequences of locally produced vaccine strains. These include work by Samad *et al.* (2025), who recently sequenced the Bangladesh vaccine strain (Samad *et al.*, 2025) after previously sequencing the parental outbreak strain (Samad *et al.*, 2024); Orynbayev *et al.* (2020), who reported the sequence of the attenuated Neethling-RIBSP strain (Orynbayev *et al.*, 2020) and Douglass *et al.* (2019), who sequenced the Herbivac LS vaccine and identified differences in the superoxide dismutase homologue compared to the Neethling vaccine strain (Douglass *et al.*, 2019). This latter study built on earlier work by Mathijs *et al.*, who in 2016 sequenced three commercially available Neethling-like vaccine strains and identified genetic differences among them (Mathijs *et al.*, 2016b).

Biswas *et al.* (2019) extended these analyses by sequencing 13 CaPV genomes to compare virulent and attenuated strains. The researchers found that several ankyrin and kelch-like proteins, as well as the variola virus B22R-like gene homolog, were frequently mutated in vaccine strains (Biswas *et al.*, 2019). Among these vaccine isolates, frameshift mutations were especially common and could potentially increase the risk of reversion to wild-type virus (Biswas *et al.*, 2019). Such studies provide an important foundation for future work using targeted molecular approaches to rationally attenuate LSDV and generate vaccine strains with improved immunogenicity while preserving sufficient replicative capacity for vaccine production.

The locally produced vaccine manufactured by Middle East for Vaccines (MEVAC) has also undergone extensive safety and efficacy validation in studies conducted in Egypt and Vietnam. Bazid *et al.* (2023) found that the Neethling-based vaccine was well tolerated even at a 10 × dose and was protective both experimentally in calves and under field conditions involving more than 4,000 cattle in Vietnam (Bazid *et al.*, 2023). However, the researchers noted substantial variation in humoral responses detected between samples and laboratories, with an overall mean positive ELISA percentage of 51.7 ± 30.6; despite this variability, estimated farm-level protection remained high at 98–100% (Bazid *et al.*, 2023). These findings further highlight the need for standardised, high-quality serological testing approaches alongside well-produced vaccines and reliable diagnostic infrastructure.

In terms of correlates of protection, a recent study linked the superior performance of Lumpy-ProVac^{Ind} compared to an Uttarkashi-strain-based GTPV heterologous vaccine to its ability to induce significantly higher titres of neutralising antibody, numbers of LSDV-specific CD8$^+$ T cells and levels of LSDV-stimulated IFN-γ *ex vivo* at 30 days post-immunisation (R. Kumar *et al.*, 2026).

Novel homologous LAVs

Several attempts to generate new and improved live attenuated LSD vaccines have been reported. Following the incursion of LSDV into India in 2019, the country adopted vaccination with GTPV owing to the lack of availability of an effective LSDV vaccine, although the efficacy of this strategy has since been questioned. To generate a locally relevant homologous alternative, Kumar *et al.* (2023) attenuated a 2019 Indian field strain of LSDV through Vero cell passage and tested it in ten calves. The resulting vaccine (Lumpi-ProVacInd) was well tolerated, stimulated both humoral and cell-mediated immunity (measured by PBMC proliferation and serum IFN-γ concentration), and protected animals from virulent challenge with a circulating field isolate at day 30 post-vaccination (Kumar *et al.*, 2023). In field trials involving more than 25,000 cattle, the vaccine was safe and induced seroconversion in 85% of animals; importantly, only 14 mild cases of LSD were reported over the following 6 months, while nearby farms experienced substantial disease burdens (Kumar *et al.*, 2023). A more recent study of the vaccine's performance in buffaloes showed that it also induced strong humoral and cell-mediated immune responses, including potent IFN-γ and CD8$^+$ recall responses *in vitro*, although protection against virulent challenge was not assessed (Dhanda *et al.*, 2024).

Another approach to the generation of novel LSDV vaccine strains relies on molecular virology and sequencing studies to identify candidate genes for rational attenuation (e.g., (Biswas *et al.*, 2019)). One study immunised cattle with LSDV lacking ORF005 or ORF008, which encode IL-10-like and IFN-γ-like products, respectively, but found that although the recombinant viruses were protective, they remained insufficiently attenuated for safe use (Kara *et al.*, 2018). A different recombinant virus lacking the virulence genes LSDV005, LSDV008, LSDV066, and LSDV142 was better tolerated in cattle at high doses, with two of three animals experiencing only mild swelling at the injection site. Moreover, a single field

dose induced high levels of neutralising antibodies and effective protection against challenge with the virulent parental strain at day 21 post-immunisation (Chervyakova *et al.*, 2022).

Identifying genes that should remain intact in attenuated strains is equally important. In 2020, Douglass *et al.* built on their previous work (Munyanduki *et al.*, 2020a) to explore the impact of disrupting the superoxide dismutase (SOD) homologue encoded by LSDV ORF131, which is mutated in the Neethling vaccine manufactured by OBP but not in Herbivac (Douglass *et al.*, 2019). In a small cattle study, the researchers found that vaccine-induced lesions were less severe in the presence of the SOD homologue and therefore argued for retention of this gene in future vaccine strains (Douglass *et al.*, 2020).

Maternal immunity following vaccination

Since 1968, it has been recognised that calves fed colostrum containing anti-LSDV antibodies may retain these protective factors for up to 6 months (Weiss, 1968), forming the basis for recommendations that calves born to immune mothers receive their first vaccination at this age.

More recent vaccine studies show that maternal LSDV-neutralising antibodies can be transferred to calves as early as 3 days after birth; however, less than 40% of approximately 20 calves in one study retained potentially protective titres at 3 months of age (Agianniotaki *et al.*, 2018). Similarly, a 2024 study in Serbia found that although almost all calves born to immune mothers received maternal antibodies via colostrum, these antibodies began to decline from around 30 days after birth and were rarely detectable by 4 months of age (Samojlović *et al.*, 2024). In line with these findings, a study in Thailand reported that only half of calves had detectable antibodies at 60 days post-birth, and none of the 37 calves tested were positive by VNT at 120 days (Rittipornlertrak *et al.*, 2024). The timing of vaccination during gestation does not appear to influence the level or persistence of maternal antibodies in colostrum-fed calves (Gaber *et al.*, 2022). Taken together, these data suggest that current recommendations for first vaccination at 6 months of age may require reassessment.

In the context of heterologous LAV use against LSDV, specific antibodies were detected in the sera of 80% of 6-month-old calves whose mothers had received multiple immunisations with SPPV vaccines (Lyapina *et al.*, 2025).

It remains unclear whether factors beyond maternal VNT influence the strength, duration, or efficacy of colostrum-derived antibodies.

Adverse events relating to current homologous LAVs

The so-called “Neethling response” is a well-documented set of adverse reactions that occurs to varying extents and frequencies among cattle immunised with the available LAVs. It is often cited as a reason to favour inactivated or subunit

vaccines, and it is therefore important to consider findings from recent studies investigating this phenomenon. In one such study, approximately 7% of cattle vaccinated with a Neethling strain LAV under experimental conditions developed skin nodules that appeared 1–3 weeks post-immunisation and resolved within the following 3 weeks (Bamouh *et al.*, 2021), while a previous large field study reported just 0.4% of cows were adversely affected (Ben-Gera *et al.*, 2015).

In fact, the frequency of cutaneous adverse events appears to vary considerably among different live attenuated LSDV vaccines and by dose. Dose dependent frequency of the Neethling response was reported in the above study by Bahmouh *et al.* (Bamouh *et al.*, 2021), and similar results were seen in studies of a GTPV LAV in goats (Esmaeili *et al.*, 2024) A 2021 study comparing five commercially available LSDV LAVs found that all were generally well tolerated, but one vaccine, LSD Neethling O vivant (from MCI Santé Animale; Morocco) produced large local injection-site reactions in just over 40% of animals (n=7), whereas the LSD Vaccine produced by OBP in South Africa did not induce any local reactions in the calves used in the study (Haegeman *et al.*, 2021a). A previous field study conducted in Greece reported local reactions in 12% of cattle vaccinated with the OBP vaccine (n=215 calves and adults combined), although this rate fell to 2% within the calf age group corresponding to that used in the Haegeman *et al.* study (Katsoulos *et al.*, 2018). Understanding the basis for these marked differences in the frequency and severity of post-vaccination skin nodules may help identify strategies to minimise vaccine-associated adverse effects.

Productivity drops may also be seen post-immunisation with Neethling-derived vaccines. One study in Bulgaria concluded that vaccination negatively affected not only milk production but also milk quality for cheesemaking (Angelova *et al.*, 2018) By contrast, a study involving more than 20,000 dairy cattle in Israel concluded that any vaccine-associated loss of milk production was “negligible” (Morgenstern and Klement, 2020).

Another important risk associated with LAVs is the potential initiation of outbreaks through either direct release of live virus or recombination events. A study of the RUSSIA/Saratov/2017 strain identified 27 recombination events consistent with the apparent emergence of this virulent strain from an attenuated vaccine strain that contained virulent recombinant virus, and which was used in neighbouring Kazakhstan (Sprygin *et al.*, 2018b). Moreover, infections may arise from recombinant LSDV strains generated during insufficiently controlled vaccine production processes, as documented for Lumpivax (Bedeković *et al.*, 2018; Haegeman *et al.*, 2021b) and the OBP LSD vaccine (Bedeković *et al.*, 2018). In Russia in 2017, large outbreaks occurred following the vaccine-related release of a recombinant clade 2 LSDV strain (Kononov *et al.*, 2019a), which subsequently spread into China and Southeast Asia (Tran *et al.*, 2021). The associated economic, animal welfare, and societal consequences of such events are substantial and underscore the importance of rigorous manufacturing and safety standards.

In addition to these risks, some commercially available vaccines are poorly defined and insufficiently tested, potentially resulting in inadequate protection. For example, Gari *et al.* (2015) reported poor protective efficacy of the locally

produced Neethling and KSGP O-180 strain vaccines used in Ethiopia (Gari *et al.*, 2015). Some LSDV vaccine batches have also been reported to contain bluetongue virus (BTV) mRNA (Bumbarov *et al.*, 2016).

Finally, vaccine potency is a critical determinant of the efficacy of LAVs, yet conventional potency testing methods based on tissue culture and *in vivo* challenge models are costly, time-consuming, and associated with biosafety and biosecurity concerns. Abousenna *et al.* (2026) recently reported a promising advance towards molecular titration using qPCR: titres obtained by qPCR from tested commercially available vaccine batches (source undisclosed) correlated strongly with tissue culture titres in MDBK cells, which in turn correlated significantly with protection in a calf challenge model (Abousenna *et al.*, 2026).

Heterologous LAVs

While homologous LAVs can be highly effective under optimal conditions, their use may prove challenging in practice because of the documented Neethling response, lack of DIVA capability, and relatively high cost, coupled with legislative or logistical barriers to acquiring sufficient vaccine stocks within the short timeframes often required for outbreak control. One possible solution is heterologous vaccination, based on the high antigenic similarity among SPPV, GTPV, and LSDV. However, these vaccines may also induce adverse effects, and their use can result in the loss of SPPV/GTPV-free status within the affected country or region.

Licensed heterologous LAVs

In some regions heterologous vaccination with GTPV/SPPV is used to protect cattle from LSDV. Notably, in the Russian Federation, SPPV LAVs are widely employed (Lyapina *et al.*, 2025); while in China, the locally produced AV41-based GTPV LAV is the method-of-choice to immunise cattle (Chang *et al.*, 2025b). Several studies have focused on defining the resulting immune response and protective efficacy.

Commercial SPPV vaccines appear to show variable efficacy against LSDV. For example, vaccination with a single dose of the Bakırköy strain SPPV vaccine failed to protect a small proportion of farms during outbreaks in Turkey in 2014–2015, although the researchers suggested that this might have been due to under-dosing (Şevik and Doğan, 2017). Similarly, SPPV vaccines underperformed in Egypt in 2016 (Abdallah *et al.*, 2018), and in Ethiopia between 2008 and 2012 (Gelaye *et al.*, 2015), as well as in studies conducted under both laboratory and field conditions (Ben-Gera *et al.*, 2015; Enul *et al.*, 2024; Hamdi *et al.*, 2020a; Norian *et al.*, 2019). By contrast, the Russian 10× Sheep Pox Cultural Dry vaccine was reported to perform satisfactorily during the 2015 outbreak in Armenia (Hakobyan *et al.*, 2024, 2023).

Despite concerns regarding the efficacy of these vaccines, several noteworthy observations have been made regarding their immunogenicity. Although only approximately half of cattle vaccinated in the field with a Bakırköy strain-derived live attenuated SPPV vaccine at five- or ten-times the sheep dose had seroconverted by day 30, the vaccine performed

well in pregnant cows in terms of inducing maternal antibodies that were efficiently transferred through colostrum to nearly 90% of calves during the first week of life. However, these antibodies were relatively short-lived, and most calves had lost detectable antibodies by 3 months of age (Enul *et al.*, 2024). Alongside this, Lyapina *et al.* (2025) characterised the humoral immune response of cattle first immunised at 6 or ≥17 months of age and revaccinated 1 year later with an SPPV LAV containing the ARRIAH strain. The researchers identified a negative correlation between age at second vaccination and ELISA seropositivity. In terms of antigen recognition, sera from approximately half of vaccine responders reacted positively to P24, P34, P40, P42, P44, P56, and P66 proteins from the parental SPPV strain, and most of these proteins were still recognised 1 year later by sera from the same animals (Lyapina *et al.*, 2025). Lastly, a recent study found that levels of vitamin D (either from sunlight exposure or supplementation) did not affect calves' humoral response to the RM/65 SPPV vaccine (Seyed Ali *et al.*, 2025)

There is growing evidence that GTPV LAVs may provide superior heterologous protection in cattle compared to SPPV LAVs. Norian *et al.* (2017) examined the cell-mediated immune response of cattle immunised with Gorgan strain GTPV or Romanian strain SPPV vaccines and found that the GTPV vaccine induced higher levels of lymphocyte proliferation and IFN-γ and IL-4 production in *in vitro* restimulation assays, as well as a higher frequency of IFN-γ mRNA-positive PBMCs in vaccinated animals (Norian *et al.*, 2017). Consistent with these findings, Gari *et al.* (2015) had previously demonstrated the efficacy of the Gorgan strain GTPV vaccine in protecting cattle against virulent challenge with an Ethiopian LSDV field isolate (Gari *et al.*, 2015), while Norian *et al.* (2019) reported strong immunogenicity of the same vaccine in calves in Bulgaria (Norian *et al.*, 2019). GTPV vaccines based on the Uttarkashi strain also performed well in cattle in India during the 2019 outbreaks (Bayyappa *et al.*, 2025a), but not during 2025 when vaccinated cattle were affected with LSDV at the same rate as unvaccinated (R. Kumar *et al.*, 2026). Another study compared locally produced live attenuated SPPV Niskhi and GTPV G20-LKV vaccine strains administered to Kazakh local breed cattle at ten-times the recommended sheep/goat dose. Although both vaccines were well tolerated and provided significant protection against challenge, the G20-LKV strain demonstrated superior immunological performance (Zhugunissov *et al.*, 2020), consistent with earlier findings from Iran (Varshovi *et al.*, 2017).

More recently, Haegeman *et al.* (2025) confirmed and extended these observations. The researchers conducted a side-by-side comparison of four commercially available live attenuated SPPV vaccines (including RM65, Romania, and Bakırköy strains) and one GTPV vaccine (Gorgan strain) for protection against virulent LSDV challenge in calves (Haegeman *et al.*, 2025). All vaccines were well tolerated, but the SPPV vaccines induced weaker and slower humoral and cell-mediated immune responses compared with the GTPV vaccine. Accordingly, at the doses tested, the SPPV vaccines failed to protect cattle challenged 21 days later, whereas the GTPV vaccine provided effective protection (Haegeman *et al.*, 2025). The researchers suggested that ex vivo whole-blood IFN-γ production by PBMCs may correlate with the differential levels of protection observed between vaccines.

GTPV vaccines may also be preferable for use in buffaloes. A large field study spanning the full lifespan of cross-bred buffaloes concluded that vaccination with the live attenuated GTPV strain AV41 was well tolerated and maintained high antibody titres for at least 5 months without negatively affecting growth, milk yield, or pregnancy (Abulaiti *et al.*, 2025).

Finally, non-natural hosts should be used with caution in immunology or vaccine studies of LSDV, and detailed methodological reporting is essential to allow meaningful comparisons between studies. For example, mice immunised with a live attenuated SPPV vaccine exhibited profound differences in immune profile and pathology depending on the route of administration (Shoulah *et al.*, 2022).

Novel heterologous LAVs

We did not find any reports of novel heterologous (SPPV/GTPV) LAVs targeting LSDV, but the reader is referred to the novel SPPV and GTPV LAVs sub-section of this report.

Adverse events relating to current heterologous LAVs

One study reported dose-dependent fever, inappetence, skin lesions, and reduced milk yields from 1-4 weeks after vaccination of cows with ten-times the sheep dose of the RM65 SPPV vaccine, but not in the unvaccinated control group or in cattle receiving one- or five- times the sheep dose (Abutarbush and Tuppurainen, 2018), while noting that this dose also induced the strongest humoral response. Similarly, Abutarbush *et al.* (2016) reported that approximately 8% of animals developed skin nodules, while almost all experienced fever, in a field study of nearly 20,000 cattle vaccinated with the RM65 SPPV vaccine Jovivac in Jordan (Abutarbush *et al.*, 2016).

There has also been a single report of liver stress in cattle following heterologous immunisation (Burkov *et al.*, 2021). This observation is interesting in light of studies of natural LSDV infection reporting elevated liver enzyme levels during disease (S. F. Ahmad *et al.*, 2023; Mahajan *et al.*, 2025; Yanni *et al.*, 2021).

Inactivated vaccines

Inactivated vaccines are typically less immunogenic than LAVs; they generally require two immunisations to be effective, and the immunity they induce may also be less long-lived. Although the production of inactivated vaccines still requires expensive high-containment facilities for the preceding live virus, the vaccine itself does not risk viral shedding, recombination, or reversion to virulence. These vaccines have therefore been proposed as a potentially safer option for disease-free areas.

After isolating LSDV from field samples using embryonated chicken eggs, Shahzad *et al.* (2025) adapted the virus for growth in MDBK cells and subsequently inactivated it using binary ethyleneimine (BEI). After formulation of the crude

inactivated virus with Montanide Immune System Activator 50 V2 adjuvant (SEPPIC), the researchers compared its immunogenicity and protective efficacy with those of an undisclosed commercially available LAV in rabbits. The inactivated vaccine elicited a strong humoral response, with a mean neutralisation titre of 1:80 compared with 1:148 in the live attenuated group, while 7/8 and 8/8 rabbits, respectively, were protected from disease following challenge (Shahzad *et al.*, 2025). Although the Montanide adjuvant is reported to induce strong T- as well as B-cell responses, this was not specifically assessed in the study.

These data broadly support earlier findings using Montanide-adjuvanted inactivated Neethling strain LSDV, which, after two immunisations, performed comparably to the equivalent LAV in terms of eliciting antibody responses and protection against virulent challenge under laboratory conditions, while also driving nearly 80% seroconversion in field settings by 28 days post-second immunisation (Hamdi *et al.*, 2020b). However, titres declined substantially by day 50 in laboratory animals and by 4 months in the field (Hamdi *et al.*, 2020b), suggesting that further optimisation is required. These observations align with more recent work indicating that biannual boosting may be necessary for inactivated LSDV vaccines, whereas LAVs maintain immunity for approximately 12-18 months, and in some cases longer (Haegeman *et al.*, 2023a).

Similarly, researchers working in Thailand reported comparable antibody titre as measured by VNT and duration of immunity after a single immunisation of calves with Lumpyvax® or two immunisations one month apart with purified BEI-inactivated LSD/THAI/CMU/21/05 (Rittipornlertrak *et al.*, 2026), though protection from virulent challenge was not assessed in this study.

Wolff *et al.* (2020) compared the effects of different adjuvants, including Polygen, MVP Adjuvants® (Omaha, USA), and a proprietary formulation comprising Amphigen, Quil A, and cholesterol. After two immunisations, cattle receiving the proprietary adjuvant formulation experienced more adverse events, including fever and injection-site reactions in three of six animals, although both inactivated vaccines protected cattle against virulent challenge as effectively as a single immunisation with an attenuated Neethling strain (Wolff *et al.*, 2020b). More recently, the same group demonstrated that a BEI-inactivated LSDV vaccine based on a Serbian field strain and adjuvanted with Polygen was highly protective in cattle, requiring only 10^4 cell culture infectious $dose_{50}$ (measured prior to inactivation) to render Holstein-Friesian cattle resistant to virulent challenge (Wolff *et al.*, 2022).

BEI inactivation is inexpensive and well established, but its preparation and use are technically demanding, and residual neutralised chemical components may remain within the final vaccine preparation. Gamma-ray inactivation of viruses for vaccine production has been successfully trialled for both bacterial (e.g., (Babb *et al.*, 2016)) and viral (e.g., (Chen *et al.*, 2021; Honnold *et al.*, 2014)) vaccines, and some groups in North Africa have begun exploring its application to LSDV (reported by (Zewdie *et al.*, 2025). Compared with chemical inactivation, gamma-ray approaches may offer several

potential advantages: while viral DNA is extensively damaged, protein epitopes may be better preserved; vaccines may be cheaper to produce; and the resulting products may exhibit greater thermostability while avoiding chemical contamination. However, regulatory challenges and the lack of standardised, validated approaches to viral inactivation and vaccine preparation remain major obstacles. The practical potential of this strategy for inactivated LSDV vaccines therefore remains unclear.

Inactivated heterologous vaccines have also been explored. Tian *et al.* (2025) compared the responses of Angus cattle to 10 sheep-doses of adjuvanted purified BEI-inactivated GTPV AV41 versus the same dose of a commercially available live attenuated GTPV vaccine (AV41 strain) (Tian *et al.*, 2025). Both vaccines induced approximately 90% seroconversion by day 28 post-vaccination, although the LAV stimulated immune responses more rapidly. An intriguing observation from this study was that vaccination with either vaccine was associated with marked alterations in gut microbiota composition: *Firmicutes* abundance increased, whereas *Bacteroidetes* abundance decreased (Tian *et al.*, 2025). Moreover, antibody titres correlated positively with *Firmicutes* abundance and negatively with *Bacteroidetes* abundance. Human and murine studies have increasingly highlighted potential effects of gut microbiota on vaccine responses (reviewed in (Decker *et al.*, 2025)), with some studies reporting up to a 30% increase in seroconversion to influenza vaccines, whereas antibiotic treatment prior to vaccination may reduce responses (reviewed in (Gioula and Exindari, 2025)). A single study in calves seems to provide further support for this concept: when calves were fed prebiotics mixed with their food then vaccinated with a live hexavalent viral vaccine (not targeting LSDV), they mounted significant $CD4^+$ T cell activation and enhanced Th1 responses compared to non-probiotic fed animals (Ikehata *et al.*, 2025).

Subunit vaccines

Subunit vaccines offer the potential to overcome many of the risks associated with LAVs while inducing immunity against carefully selected pathogen antigens. They may also enable DIVA by detecting immunity to viral antigens not present in the vaccine, exclusively in animals that have been infected.

The selection of optimal antigens for next-generation LSDV vaccines remains challenging, partly because protective immunity in natural hosts is still incompletely understood. A recent review integrated findings from multiple studies and used orthopoxvirus data to infer likely CaPV correlates where direct evidence was lacking. The researchers identified the most promising antigen candidates: *LSDV ORF024 (VACV F9L), LSDV ORF059 (VACV G9R)*, *LSDV ORF060 (VACV L1R), LSDV ORF074 (VACV H3L), LSDV ORF104 (VACV A13L), LSDV ORF105 (VACV A14L), LSDV ORF109 (VACV A17L), LSDV ORF117 (VACV A27L), LSDV ORF118 (VACV A28L), LSDV ORF122 (VACV A33R), LSDV ORF123 (VACV A34R), LSDV ORF126 (VACV A36R),* and *LSDV ORF141 (VACV B5R/C3L)* (Teffera *et al.*, 2025). A different group also showed the potential for purified and adjuvanted LSDV ORF075 and ORF090 proteins to elicit immune responses in mice (Gu *et al.*, 2025), though whether the same proteins would be immunogenic in cattle remains to be seen.

Among the above possible targets, several studies have provided further evidence in their favour. Ren *et al.* (2026) described the generation of a cross-CaPV-neutralising murine monoclonal antibody recognising a continuous linear epitope within the LSDV ORF123 protein (Ren *et al.*, 2026). ORF117 was similarly highlighted in a study by Yu *et al.* (2026) who generated two monoclonal antibodies specific for different epitopes within this protein, which subsequently bound whole viral particles *in vitro* (Yu *et al.*, 2026)

Rani *et al.* (2025) recently reported the computational design of a molecularly adjuvanted multi-epitope subunit vaccine comprising conserved immunodominant CTL-, TH cell-, and B-cell epitopes from the GPCR, p32, and RPO30 proteins of Indian LSDV isolates (Rani *et al.*, 2025). These antigens were predicted to bind major bovine leukocyte antigen (BoLA) alleles as well as TLR4, and vaccine production could potentially be scaled using *Escherichia coli* expression systems (Rani *et al.*, 2025). However, the vaccine has not yet been evaluated *in vivo*.

Another computationally designed multi-epitope vaccine incorporated 23 B- and T-cell epitopes derived from LSDV proteins P35, A4L, A33R, and L1R together with a molecular adjuvant and demonstrated strong predicted TLR4 binding (A. Kumar *et al.*, 2025). Similarly, a separate multi-epitope vaccine comprising predicted B- and T-cell epitopes from the LSDV membrane glycoprotein was predicted to be highly immunogenic (Salauddin *et al.*, 2024). Earlier, Kar *et al.* (2022) used bioinformatics approaches to design a vaccine around predicted B-cell and $CD8^+$ T-cell epitopes within four highly conserved LSDV proteins (LSDV031, LSDV090, LSDV103, and LSDV109), again with strong predicted immunogenicity (Kar *et al.*, 2022). Notably, LSDV109 was also highlighted among the candidate antigens identified by Teffera *et al.* (Teffera *et al.*, 2025). Data from *in vivo* testing of these next-generation vaccines are awaited with considerable interest.

It is worth noting that the antigens identified and trialled in the above studies could also be used as the basis for the development of mRNA vaccines.

Multivalent vaccines

Multivalent vaccines are particularly attractive in resource-limited settings because they allow farmers to immunise their livestock against multiple pathogens simultaneously, thereby helping to raise immunisation rates to the critical level required for herd immunity.

A combined LAV targeting LSD, contagious bovine pleuropneumonia, and Rift Valley fever performed well under laboratory conditions and was subsequently trialled in a large field study in Burkina Faso, where it was similarly well tolerated (Bamouh *et al.*, 2024). Unfortunately, incidence data for LSD were not collected during the field study, and so large-scale efficacy remains to be established.

Preliminary safety and immunogenicity data also suggested promise for a bivalent LAV targeting Mycoplasma mycoides subsp. mycoides, the causative agent of contagious bovine pleuropneumonia, together with LSDV. Holstein cattle (n=48) were immunised either with the experimental vaccine or with the corresponding single-pathogen LAVs and monitored for 90 days. Vaccinated animals mounted strong and durable immune responses from as early as 7 days post-vaccination, and combining the vaccines did not reduce immunogenicity against either pathogen (Safini *et al.*, 2022). However, duration of immunity and protective efficacy remain to be determined.

Encouraging immunological responses were also reported following prime-boost vaccination of cattle with a recombinant LSDV expressing bovine ephemeral fever virus genes. Immunised animals were protected from virulent LSDV challenge while also mounting antibody titres predicted to be protective against bovine ephemeral fever virus (Douglass *et al.*, 2021). Similarly, building on earlier work (Wallace *et al.*, 2006; Wallace and Viljoen, 2005), Wallace *et al.* (2020) used a recombinant LSDV expressing two protective glycoprotein genes from Rift Valley fever virus to immunise calves under laboratory conditions, demonstrating both safety and efficacy in generating protective immunity against both pathogens (Wallace *et al.*, 2020). Issabek *et al.* (2025) also reported promising immunogenicity in mice using a rationally attenuated recombinant LSDV lacking genes encoding immunomodulatory proteins (LSDV005, LSDV008, or LSDV066) and expressing bovine IL-18 as a model antigen (Issabek *et al.*, 2025). However, results obtained in non-natural host species should be interpreted cautiously.

Es-Sadeqy *et al.* (2021) additionally reported the development and testing of a multivalent BEI-inactivated vaccine targeting both BTV and LSDV in cattle. Prime-boost vaccination elicited high titres of neutralising antibodies against both pathogens, which persisted for up to 12 months post-boost in 16 of the 20 animals tested (Es-Sadeqy *et al.*, 2021), although direct protective efficacy against LSDV was not assessed.

Finally, Tareq *et al.* (2025) adopted an interesting approach to multiepitope vaccine design by selecting antigens conserved among LSDV, GTPV, and SPPV. Using bioinformatics tools, the researchers identified nine MHC-I, MHC-II, and B-cell epitopes and generated a bacterially expressed vaccine construct with strong predicted immunogenicity (Tareq *et al.*, 2025). This vaccine has not yet been evaluated *in vivo*.

See also (Hurisa *et al.*, 2024) in the SPPV/GTPV vaccines section, Multi-valent vaccines sub-section.

Vectored vaccines

We did not find any reports of vectored vaccines targeting LSDV; this area of development is impeded by the lack of known protective antigens for the virus.

DIVA-enabled vaccines

A safety and efficacy study in calves showed that, although the inactivated vaccines tested were only moderately potent under the study conditions, inclusion of keyhole limpet hemocyanin within the vaccine formulation effectively functioned as a positive DIVA marker (Ronchi *et al.*, 2024). More recently, the group confirmed the safety and immunogenicity of the same vaccine in lactating dairy cows and reported that milk quality and quantity were not impacted by vaccination (Testa *et al.*, 2026). While not broadly applicable to the current situation, this study re-highlights the potential for the development of vaccines including marker antigens to enable DIVA.

Vaccine production

Production of LSDV LAVs in cell culture is generally performed using MDBK cells. However, it has long been recognised that many such cultures are contaminated with bovine viral diarrhoeal virus, and eliminating this contamination requires the laborious process of serial passage through embryonated hens' eggs (Munyanduki *et al.*, 2020b). Several studies have therefore explored alternative cell lines for the production of recombinant or passage-attenuated LSDV vaccines. The baby hamster kidney-21 cell line was permissive to recombinant LSDV, whereas a rabbit kidney cell line required the addition of a vaccinia host range gene to permit viral growth (van Diepen *et al.*, 2021). In another study, cell lines derived from embryonic sheep skin were found to be the most permissive, achieving titres comparable to those observed in primary ovine heart, kidney, and lamb testis cells (Rhazi *et al.*, 2021a).

The same group also reported approximately two-fold higher viral yields for LSDV grown in primary lamb testis cell cultures using a CelCradle™500A bioreactor compared with conventional Cell Factories (Rhazi *et al.*, 2021b). More recently, You *et al.* (2024) found that the murine osteoblastic cell line MC3T3-E1 was permissive to LSDV replication (You *et al.*, 2024), suggesting potential utility for *in vitro* studies and possibly future vaccine production.

Conclusions

The rapid spread of LSD across the Middle East, Asia, and Europe has drawn a great deal of attention to this disease, particularly since its emergence in Turkey in 2013. The studies discussed here represent some of the many significant advances that have been made over the past decade in the study of LSD biology, host-pathogen interactions and immunology, epidemiology, and control measures. These advances, including the characterisation of LSDV proteins, identification and modelling of viral transmission patterns, and development of new vaccines and therapeutics, strengthen our position in the effort to control LSD and reduce its economic impact on a global livestock farming system that is under increasing strain. However, many gaps remain in our understanding of the virus and ability to control it. Many of these are economic: the endemic status of LSDV in resource-limited regions of Africa and Southeast Asia, beyond the reach of most surveillance programmes, creates critical blind spots in our ability to predict viral evolution and epidemiology while impacting the livelihood of affected farmers and other stakeholders.

LSD already threatens some of the world's top cattle producers (e.g., China, the European Union, India, and Russia), and its transmission across national borders places other countries at risk as well. The huge increase seen in the number of LSD studies published over the past decade will likely continue into the next. Hopefully, these efforts will be matched by regulatory and policy decisions aimed at fostering the international cooperation required to control this transboundary disease, while focusing surveillance and disease control resources to remote, resource-limited regions where they are most needed to protect particularly vulnerable populations from the burdens imposed by LSD.

Future research priorities

Based on the available literature, expert opinion, and previously published reviews, we suggest that the following areas of research into lumpy skin disease virus should be considered high priority:

Biology of the pathogen

- Continuing *in silico* modelling of viral protein structures and interactomes, coupled with validation *in vitro*.
- Validation and comparison of results obtained in different cell lines and *in vitro* vs. *in vivo*.
- Monitoring and genetic sequencing of new and historical variants to understand the frequency of viral recombination and reversion to virulence in vaccine strains.

Diagnosis

- Conclusive identification of the optimal antigens for CaPV serology via well-conducted comparative studies utilising a broad range of relevant samples
- Complete testing of novel DIVA assays to establish their range of applicability and accuracy under different situations including different sample types and virus/vaccine combinations, as conducted by Byadovskaya and colleagues in 2020 for the then-available commercial and published tests (Byadovskaya *et al.*, 2020).
- Validation of new serological tests on large sample-sets; favouring protocols that are easy to use in low-resource settings without specialised biosafety facilities.
- Development of integrated control program where vaccination/diagnostics/DIVA/molecular monitoring of emerging strains work together to eradicate/manage disease.

Pathogenesis

- Uncovering the genetic/molecular determinants of viral virulence, especially in outbreaks with particularly high levels of mortality in infected animals.
- Characterisation of the host/pathogen factors and interactions that determine LSD severity (including subclinical disease).

Immunology

- Comprehensive studies of the immune response to natural infection, especially of the immunology of sub-clinical infection and the maintenance of natural protective immunity, as well as of the identification of protective antigens. These studies form the necessary foundation for the development of effective and safe next-generation vaccines and should be accorded a high priority.
- Comparative studies of immunity to LAVs versus natural infection, aiming to identify ways to render vaccines more immunogenic. Similarly for maternal immunity to vaccines versus natural infection.

- Studies aiming to understand the genetic basis for the differential susceptibility of cattle breed to LSD. Such information could prove valuable in planning selective breeding programs for increased disease resistance, and could also provide a rational basis for further work on the differential responses of cattle breeds to vaccines.

Epidemiology

- Intensified study of viral circulation and transmission patterns in low- and middle-income endemic areas (e.g., in sub-Saharan Africa and Southeast Asia).
- Establishment and strengthening of disease surveillance networks and international data sharing capabilities in countries recently exposed to LSDV or at risk of viral introduction via transboundary animal movements.
- Increasing development of participatory epidemiology to incorporate local sociocultural and economic situations into the development of surveillance networks, disease control strategies, etc.
- Vector- and host-specific information on the role of insects in LSDV transmission under different environmental and animal management conditions.
- Continuing study of the potential role of wild ruminant species in the maintenance and transmission of LSDV.

Control

- Further research on the possible link between microbiota, antibiotic over/mis- use and lower responses to veterinary vaccines, including the potential use of probiotics/prebiotics to improve vaccine responses.
- Investigation of the potential for vectored and mRNA vaccine approaches, dependent upon prior identification of protective antigens (as discussed in (Mahony *et al.*, 2024)).
- A focus on generating vaccines that are not only effective but also: have a clear pathway to being affordable and available; whose use would not compromise the ability of the affected country to trade (i.e. inactivated or DIVA-enabled); are thermally stable and easy to apply.
- Lack of well-trained and experienced veterinarians in affected regions is a significant problem for transboundary disease control.
- Studies that assess barriers to vaccination for farmers and evaluate strategies to overcome them.

Sheeppox and goatpox viruses

Introduction

Together with LSDV, sheeppox virus (SPPV) and goatpox virus (GTPV) comprise the genus *Capripoxvirus*. Like LSDV, SPPV and GTPV are dsDNA viruses transmitted through contact among infected animals, with anthropogenic movement of sheep and goats playing a major role in their intra- and international spread. The clinical signs of sheeppox (SPP) and goatpox (GTP) in sheep and goats, respectively, are similar to those of LSD in large ruminants. Alongside the characteristic skin lesions, both diseases can present with fever, lethargy, lameness, and many other nonspecific symptoms that broadly reduce animal fitness, welfare, and productivity (Simpson *et al.*, 2023). The morbidity and mortality rates associated with SPP and GTP vary depending on breed, farming/animal management, and other genetic and environmental variables, but they are typically higher than the corresponding rates in LSDV-infected cattle, with a commensurately greater relative impact on economic stability in small ruminant farming communities (Limon *et al.*, 2020).

Both SPPV and GTPV are endemic across much of Africa and Asia, with the past decade seeing increasing transmission into Southeast Asia and recurring outbreaks in vulnerable areas of eastern Europe. SPP and GTP were historically present in western Europe but were eradicated in the 1960s; however, a series of outbreaks in Spain in 2022-2023 emphasised that both viruses pose a real threat to non-endemic regions, requiring renewed attention to all aspects of SPPV and GTPV research including their virology/molecular biology, host-pathogen interaction networks and epidemiology in endemic and non-endemic areas. Strategies for disease surveillance and control, including the development of vaccines that effectively protect animals from SPP and GTP while minimising the risks of reversion to virulence, are an important priority. This section of the report will discuss these and other areas of ongoing SPPV/GTPV research and the advances made therein since 2015. As SPPV and GTPV have historically received substantially less research attention compared to LSDV, readers are encouraged to consult the previous section for general information on CaPV research and as a point of comparison for the progress made over the past decade.

Literature review

Biology of the pathogen

Proteomics and gene characterisation

As with LSDV, the number of uncharacterised SPPV and GTPV proteins poses a barrier to understanding their biology and to the development of effective diagnostics, vaccines, and therapeutics. Studies have begun to address gaps in our understanding of these proteins, often starting with homologues of known VACV proteins. Dashprakash *et al.* conducted sequence analysis of SPPV and GTPV ORF117, a homologue of VACV A27L, reporting a high antigenic index and surface probability (Dashprakash *et al.*, 2015). Madhavan *et al.* characterised CaPV ORF095 (a homologue of VACV A4L) and identified species-specific residues unique to LSDV, SPPV, and GTPV (Madhavan *et al.*, 2020), facilitating later incorporation of this protein into a diagnostic ELISA (discussed in more detail in the Diagnostics section below).

Most poxviruses express two families of eIF2α homologue proteins that inhibit host protein kinase R, a key mediator of the innate antiviral response. The K3 family, thought to inhibit phosphorylation of eIF2α, has also been implicated in host specificity (Cao *et al.*, 2020). SPPV protein 011 contains several mutations relative to the orthologous VACV K3 protein that are responsible for its distinct pattern of species-specific protein kinase R inhibition (Park *et al.*, 2025).

Suraweera *et al.* analysed the crystal structure of SPPV protein 14, which inhibits the Bcl-2-mediated apoptosis pathway (Suraweera *et al.*, 2020). They found that the protein binds as a monomer to the apoptosis-regulating Bax and Hrk proteins through an unusual ionic interaction, thereby blocking their proapoptotic activity (Suraweera *et al.*, 2020).

Cell culture and viral replication

Several recent studies have explored different cell lines to improve the efficiency, reproducibility, and convenience of CaPV propagation. Rhazi *et al.* compared the feasibility of propagating CaPVs in four types of primary lamb cells (heart, skin, testis, and kidney) and three cell lines (Vero cells, OA3.T fetal sheep testis cells, and ESH-L embryonic sheepskin cells), reporting superior sensitivity in the ESH-L cell line (Rhazi *et al.*, 2021a). Alongside LSDV, the immortalised hTERT-bovine ovarian duct epithelial (bOEC) cell line was also found to be susceptible to SPPV and GTPV infection, with infected cells exhibiting similar patterns of differential gene expression (H. Zhang *et al.*, 2025). Wang *et al.* recently reported that the murine osteoblastic cell line MC3T3-E1, previously found to support LSDV infection (You *et al.*, 2024), can also be productively infected by GTPV, potentially providing new opportunities for molecular biology studies (Wang *et al.*, 2026).

A baculovirus expression system using *Trichoplusia ni* insect cells was found to be superior to *E. coli* for expression of GTPV proteins, specifically the immunodominant A27L and P32 proteins (Kushwaha *et al.*, 2025). Finally, Zhang *et al.* identified and characterised a bidirectional promoter region in the GTPV genome, termed PbVV (±), which may facilitate the development of multivalent vaccines based on recombinant GTPV (Zhang *et al.*, 2017).

Geographic distribution, epidemiology, and surveillance

SPPV and GTPV are endemic across much of northern Africa, the Middle East, the Indian subcontinent, and Asia. Outbreaks are also observed in regions bordering endemic zones, including the Caucasus and the Balkans. Although these viruses were historically present in Europe and subsequently eradicated from many developed countries, the geographical ranges of both diseases have recently begun expanding, particularly into Southeast Asia.

Bianchini *et al.* recently published a comprehensive analysis of worldwide trends in the distribution of SPP and GTP between 2005 and 2022 (Bianchini *et al.*, 2025). Among many notable findings, the researchers reported that 75% of countries reporting SPP and/or GTP were endemic or highly endemic, and of these, 85% were developing countries classified as low- or lower-middle-income, with nearly all high-income endemic countries located in the Middle East. The researchers concluded that, despite being notifiable diseases, SPP and GTP are generally neglected until a major outbreak or incursion occurs, and that quantitative epidemiological data remain severely lacking (Bianchini *et al.*, 2025).

Global situation

Africa

SPP is widespread across northern Africa, causing sporadic outbreaks among the pastoral and transhumance farming systems common to the region (Ben Chehida *et al.*, 2018; Saidi *et al.*, 2023). Limited access to adequate veterinary services has been associated with lower levels of SPP vaccination in Egypt (El-Bagoury *et al.*, 2021). A study of SPP surveillance in Tunisia between 2008 and 2017 reported rising prevalence (from an average of 14 to 24 outbreaks per month over the study period) despite vaccination efforts, although vaccination rates fell below the recommended 80% coverage between 2013 and 2016 (Kalthoum *et al.*, 2020). In Algeria, vaccination against SPP and GTP has been practised since the 1980s, and reported sheep vaccination coverage reached 75% in 2014 and 2015; however, both diseases continue to persist and are associated with substantial economic losses (Bencherik *et al.*, 2020; Kardjadj, 2017). A 2019 study reported an average of 44.9 SPP outbreaks per year across the country (Kali *et al.*, 2019).

Morocco experienced a severe SPP epizootic in 2010, and clinical presentation and initial sequencing suggested a potential link to the SPPV vaccine strain used in the country. Later phylogenetic analysis indicated that, although a single SPPV strain was likely responsible for the epizootic, it was unrelated to the vaccine strain (Haegeman *et al.*, 2016). The disease remains endemic in Morocco (Mahari *et al.*, 2024). GTP has not been reported in Morocco, Algeria, or Tunisia despite the large goat populations present in each country (Hamdi *et al.*, 2021a).

Odoom *et al.* recently published the first comprehensive study of SPPV in Ghana, where a series of outbreaks in the Upper East region in 2023 caused 75% morbidity and 37% mortality among affected sheep populations (Odoom *et al.*, 2025).

CaPVs are endemic in Nigeria (Adedeji *et al.*, 2021, 2019). In a retrospective study of outbreaks between 2017 and 2018 in Bauchi State, Limon *et al.* reported substantially higher median incidence risks and fatality rates of SPP and GTP in small ruminants (53% and 34% in sheep and 50% and 33% in goats, respectively) compared with LSD in cattle; these diseases also reduced the sale price of affected small ruminants by approximately 57% (Limon *et al.*, 2020). Similar morbidity and mortality levels were documented in a later SPP outbreak in Kaduna State (Hussaini *et al.*, 2025). A participatory rural appraisal conducted in Plateau State estimated annual losses of approximately 922 USD (~682 GBP) due to disease treatment and approximately 2,730 USD (~2,018 GBP) due to mortality on GTP-affected farms (Bolajoko *et al.*, 2019).

SPP and GTP are also endemic in Uganda, where disease control and surveillance capabilities are limited (Gerald *et al.*, 2025; Nizeyimana *et al.*, 2023). Available epidemiological data indicate approximately four outbreaks per year in the country, with very low overall prevalence but a case fatality rate of approximately 32% (Nizeyimana *et al.*, 2023).

Small ruminants comprise a significant component of livestock-based livelihoods in Ethiopia (Birhanu *et al.*, 2022), but CaPVs are widespread and impose substantial economic costs on farmers (Guash *et al.*, 2017; Kenubih *et al.*, 2021; Taye *et al.*, 2017). A number of studies have been conducted to estimate morbidity and mortality rates and identify outbreak risk factors, particularly in northern regions of the country (Aregahagn *et al.*, 2021; Kassa *et al.*, 2024; Tadesse *et al.*, 2022; Wondimu *et al.*, 2021). Tadesse *et al.* recently reported on the epidemiology of SPP and GTP in the Amhara region, using a generalised linear model to estimate viral reproduction numbers (R_o) of 1.84 and 3 for combined outbreaks within the South Wollo zone between 2013 and 2019 (Tadesse *et al.*, 2024). One of the few vaccination surveys available from Ethiopia, conducted in the Alamata district of the Tigray region, reported an average vaccination coverage of only approximately 53% for SPP and GTP between 2009 and 2014 (Tadege and Afera, 2016).

Mixed infections between CaPV and PPRV were found to be common in the eastern Democratic Republic of the Congo (Birindwa *et al.*, 2017). SPP and GTP seem to be far less prevalent south of the Equator (Kimeli *et al.*, 2025); for example,

a seroprevalence study on the Tanzania–Zambia border found that close to 0% of analysed sheep and goats were positive for SPPV or GTPV, far below the prevalences reported for other major small ruminant viral pathogens such as foot-and-mouth disease virus and PPRV (Lysholm *et al.*, 2022).

Asia and the Middle East

SPP and GTP are endemic across the Middle East (Mirzaie *et al.*, 2015), although our ability to monitor and control these diseases remains sharply limited across much of the region. SPP was first reported in Iraq by at least 2018 (Muhaidi *et al.*, 2018); a recent study from Mosul reported 10–40% morbidity and 2–6% mortality among sheep due to SPP, and phylogenetic analysis of 10 circulating strains identified >99.7% sequence identity with isolates from India, Germany, and Russia (Al-taliby *et al.*, 2025). SPPV strains have also been characterised in the Kurdistan region of Iraq (Rashid *et al.*, 2017). In Iran, CaPV is a major cause of goat culling (Didarkhah *et al.*, 2019).

SPP and GTP are both known to occur in Saudi Arabia, although epidemiological data remain limited (El-Sabagh *et al.*, 2020; Hamouda *et al.*, 2017). At least four CaPV variants appear to be circulating among sheep in Saudi Arabia (Abdellatif *et al.*, 2025). Both diseases seem to be particularly prevalent in Riyadh Province, where they frequently co-occur with PPR (Boshra *et al.*, 2015a). In 2024, the United Arab Emirates reported its first documented GTP outbreak, involving captive wild Barbary sheep (*Ammotragus lervia*), Nubian ibex (*Capra nubiana*), Arabian oryx (*Oryx leucoryx*), and scimitar oryx (*Oryx dammah*) in a fenced mountainous reserve (Hebel *et al.*, 2026).

SPP and GTP are also endemic in Kazakhstan, where outbreaks have been recorded regularly since 1961 (Abdolla, 2023). The vast majority of small ruminant farming in the country occurs in small-scale and backyard systems, which are concentrated near international borders (Abdolla, 2023). These borders likely facilitate transboundary virus spread; for example, a CaPV was identified as the cause of several animal deaths on a sheep farm in Kyrgyzstan (Aldaiarov *et al.*, 2016). However, overall understanding of pox epidemiology and transmission networks in Central Asia remains limited.

There were no officially confirmed cases of SPP in Mongolia between 2019 and 2024, but subsequent identification of SPPV in a clinically ill animal in the Almaty region indicated continued maintenance of the disease within the local sheep population (Azanbekova *et al.*, 2025). Circulating strains in Mongolia appear closely related to isolates from China (Enkhbaatar *et al.*, 2020).

SPP is endemic across India (Roy *et al.*, 2015; Suresh *et al.*, 2022), which contains the second-largest sheep population in the world (FAOSTAT, 2021). The immunosuppressive effects of CaPV infection may also contribute to increased susceptibility to co-infection with pathogens such as orf (contagious ecthyma), theileriosis, and anaplasmosis (Konappan *et al.*, 2017). A recent study of SPP outbreaks in Karnataka State reported ~11% PCR positivity among sheep, with an average mortality of 4.72% that varied widely across study regions (Reddy *et al.*, 2024a). Transmission of SPPV from

migratory to non-migratory sheep during summer grazing periods has been linked to the establishment of new endemic niches in the Western Himalayas (Chahota *et al.*, 2022). Phylogenetic analysis of Indian SPPV isolates has indicated very high sequence identity with strains from Egypt and China (Vitthal *et al.*, 2022), although reliance on single-gene sequencing may underestimate viral evolution (Yu *et al.*, 2021).

GTP is also endemic in India and imposes a substantial economic burden on regional farmers (Hegde and Deo, 2017; Moudgil *et al.*, 2025). Previous studies have indicated the presence of SPPV and GTPV strains capable of cross-species transmission (Santhamani *et al.*, 2015). Transmission of GTP has been linked to local grazing practices that facilitate introduction into naïve populations within affected regions (Hopker *et al.*, 2020, 2019), and its geographical range within India seems to be expanding (Bora *et al.*, 2021b).

GTP was first reported in Vietnam in 2005 (Babiuk *et al.*, 2008a), and outbreaks have continued since then, with unmonitored animal movement across the China–Vietnam border considered an important transmission pathway (Pham *et al.*, 2021). In an assessment of a major GTP outbreak that began in 2014 in Ninh Binh Province, Pham *et al.* reported an overall prevalence of nearly 80% in goats, with higher levels of infection associated with younger animals (3–6 months old) and those reared under free-range conditions (Pham *et al.*, 2020). Mortality reached nearly 92% in some affected goat populations (Pham *et al.*, 2021).

Finally, SPP and GTP are both responsible for substantial economic losses in Bangladesh, where morbidity in northern and central regions has been reported to range from 70–90% (Salauddin *et al.*, 2025). Co-infections with PPR have also been identified (Sultana *et al.*, 2022).

Eurasia and Europe

SPP outbreaks occur sporadically in Russia, and their frequency appears to be increasing (Sprygin *et al.*, 2023b). Phylogenetic analysis of circulating strains has indicated the presence of two distinct SPPV clusters: one in Central Russia, related to isolates previously detected in the European region of the country, and another in the Far East that is more closely related to Southeast Asian isolates (Krotova *et al.*, 2022c; Sprygin *et al.*, 2023b).

SPP is endemic in Turkey (Karapinar *et al.*, 2017). Specific spatiotemporal clusters with relatively high outbreak likelihood have been identified (Şener and Türk, 2023), and transboundary transmission has been proposed as a likely route for viral introduction into other areas of Europe. SPPV has remained exotic to most of the EU since the late 1960s (Villalba *et al.*, 2024). However, outbreaks continue to occur in eastern countries bordering endemic regions (Tuppurainen *et al.*, 2017). Greece and Bulgaria both experienced sporadic SPP outbreaks between 2013 and 2023. The following year saw a major regional epidemic emerge in both countries, alongside smaller outbreaks in Serbia, Romania, and North Macedonia (EFSA *et al.*, 2026; Yordanov and Petrishki, 2026). More than 260,000 sheep and goats (~2% of the national herd) had

reportedly been culled in Greece by September 2025 (Papadimas, 2025), rising to ~470,000 by January 2026 (Koutroumpis, 2026) and causing significant economic losses including a ~10% drop in feta cheese production during the first two months of 2026 (Charontakis, 2026).

In September 2022, Spain recorded its first confirmed case of SPP in more than 50 years, and the resulting series of 30 outbreaks lasted approximately 8 months across the affected autonomous communities of Andalusia and Castilla-La Mancha (Germán *et al.*, 2024; Villalba *et al.*, 2024). Clinical presentation during these outbreaks differed substantially from that typically reported in endemic regions, including lower animal-level mortality and a longer incubation period that facilitated silent spread of SPPV among herds (Germán *et al.*, 2024). Phylogenetic analysis indicated that these European isolates grouped within clade A2, which includes strains circulating in North Africa and the Middle East (Breman *et al.*, 2024).

Kosovo reported its first outbreak of sheep and goat pox on a sheep farm in the Ferizaj District on 15 April 2026 (BEACON, 2026).

Modes, routes, and drivers of GTP and SPP transmission

Anthropogenic movement of infected animals is a primary driver of SPP and GTP transmission (reviewed in (Kimeli *et al.*, 2025)). For example, outbreaks in Mongolia and Vietnam have both been phylogenetically linked to circulating strains in China (Enkhbaatar *et al.*, 2020; Pham *et al.*, 2020), while within China, an SPP outbreak in Gansu Province was attributed to importation of clinically ill sheep from nearby Jingyuan County (Su *et al.*, 2015).

The role of semen in transmission is not known and has not been investigated, though SPPV and GTPV can propagate in OA3.T sheep testis cells. It is likely that, as with LSDV, both viruses are shed in the semen of infected animals, but this has not been evaluated.

The role of mechanical transmission through vectors is not completely understood. Experimental infection studies are able to demonstrate transmission through vectors; however, the transmission spread of SPPV and GTPV behave differently compared to LSDV with respect to spread into new regions.

As with LSD, the potential role of wildlife in the epidemiology of GTP and SPP remains unclear. GTPV infection has been detected in wild red serow (*Capricornis rubidus*) in Mizoram, India (Bora *et al.*, 2018; Dutta *et al.*, 2019), and spillover from domestic goats to wild Himalayan goral (*Naemorhedus goral*) has been reported in the neighbouring state of Arunachal Pradesh (Bora *et al.*, 2021a). Barbary sheep (*Ammotragus lervia*), Nubian ibex (*Capra nubiana*), Arabian oryx (*Oryx leucoryx*), and scimitar oryx (*Oryx dammah*) were affected in an outbreak of GTP in the United Arab Emirates in

2024 (Hebel *et al.*, 2026). Expanded wildlife surveillance and additional studies of free-ranging caprine populations will be necessary to clarify whether wild species contribute meaningfully to GTPV and SPPV transmission (Gortázar *et al.*, 2022). Furthermore, the genes involved in host tropism of SPPV and GTPV for sheep and goats remain unknown.

Chahota *et al.* recently compared 17 SPPV and 11 GTPV field strains with host-specific native reference strains, identifying hotspots of genetic variation in genes associated with virulence, host adaptation, and immune evasion (Chahota *et al.*, 2026). One GTPV strain in particular (GTPV-Yemen) exhibited high genomic plasticity, indicating a potentially growing risk of transboundary and cross-species viral transmission (Chahota *et al.*, 2026).

Surveillance

In their retrospective analysis of the 2022–2023 SPP outbreaks in Spain, Villalba & Haegeman *et al.* reported that PCR analysis of pooled oral swab samples was a sensitive approach for identifying infected farms, whereas serology by ELISA was less useful (Villalba *et al.*, 2024). However, only two of the six outbreaks were identified through laboratory testing before clinical signs became apparent (Villalba *et al.*, 2024).

Diagnosis

As for LSD, SPP and GTP require laboratory diagnostics to differentiate their symptoms from those caused by other pathogens, such as orf virus and peste des petits ruminants virus (PPRV). However, the situation is further complicated by the propensity of some SPPV/GTPV strains to cross-infect species, particularly in settings where sheep and goats are housed together. The WOAH lists currently validated diagnostic tests and the reader is referred to this resource for further details on those approaches (WOAH, 2025).

Nucleic acid-based diagnostics

DNA diagnostics remain the first-line approach for conclusive identification of SPPV and GTPV, with recent advances relating primarily to differentiation between the two viruses.

Quantitative PCR

Researchers in China reported the development of a duplex PCR assay able to differentiate between SPPV and GTPV based on detection of the E10R and RPO132 genes; in SPPV, both genes are amplified, whereas in GTPV only the E10R

primers match the gene sequence. The assay performed well in field samples from infected sheep and goats and represents a sensitive, specific, and inexpensive diagnostic tool (Zhao *et al.*, 2017).

Assays capable of detecting more than one pathogen offer practical and economic advantages, particularly in settings where mixed infections are common. In 2019, Xu *et al.* developed a TaqMan-based assay that detected PPRV, foot-and-mouth disease virus, GTPV, and orf virus with high sensitivity and specificity when tested on a small panel of field samples (Xu *et al.*, 2019). This followed earlier work by He *et al.* in 2017, who described a multiplex RT-PCR/PCR assay able to distinguish foot-and-mouth disease virus, BTV, PPRV, SPPV, GTPV, and orf virus with high analytical sensitivity (limit of detection: 100 pg viral genomic material) and specificity when tested on a mixture of all six viruses, while also performing well on field samples (He *et al.*, 2017).

See also studies described in the LSDV diagnostics (Quantitative PCR sub-section), including (Armson *et al.*, 2015; Das *et al.*, 2017; Korthase *et al.*, 2022; Nan *et al.*, 2023; Wen *et al.*, 2023).

Loop-mediated isothermal amplification (LAMP)

The advantages of LAMP in low-resource settings apply equally to SPPV and GTPV as to LSDV, although the approach remains comparatively less developed for these viruses.

As noted above, the novel CaPV LAMP assay evaluated in Iran in 2024 demonstrated 100% diagnostic sensitivity for SPPV and GTPV, although only LSDV field samples were tested (Edrisi *et al.*, 2024).

Venkatesan *et al.* previously evaluated a novel CaPV DNA polymerase-based LAMP assay using 200 geographically diverse sheep and goat serum samples collected across India. Compared with qPCR, the assay demonstrated 97% diagnostic sensitivity and 100% specificity (Venkatesan *et al.*, 2016).

See also studies described in the LSDV diagnostics (Loop-mediated isothermal amplification sub-section), including (Batra *et al.*, 2015; Edrisi *et al.*, 2024).

Recombinase polymerase amplification (RPA) assay

Researchers in China developed an RPA-based assay targeting the CaPV GPCR gene to detect SPPV and GTPV with both real-time and lateral-flow readout options. The assays had a limit of detection of 300 copies per reaction, required only 20 minutes at 38°C, and demonstrated high specificity for CaPV in a range of ovine tissue samples (Yang *et al.*, 2017)

See also studies described in the LSDV diagnostics section, (RPA subsection), including (Cao *et al.*, 2023b; Liu *et al.*, 2023).

Nanopore sequencing

See (Eltom *et al.*, 2021), described in the LSDV diagnostics section (Nanopore sequencing sub-section).

Real-time high-resolution melting (HRM) PCR

See (Pestova *et al.*, 2018), described in the LSDV diagnostics section (Real-time high-resolution melting (HRM) PCR sub-section).

Protein diagnostics

The protein-based diagnostic approaches explored for LSDV (Kassem *et al.*, 2024) have yet to be explored for GTPV or SPPV.

Serological assays

Although SPPV and GTPV are serologically indistinguishable owing to their high degree of homology, CaPV serology can form an important component of disease surveillance. The gold-standard serological test remains the virus neutralisation test (VNT), although this approach is time-consuming and requires the use of live virus. Efforts have therefore focused on the development and validation of novel ELISAs, often benchmarked against the commercially available ID-Vet ELISA.

ELISA

Although a commercial CaPV antibody ELISA is available, some studies have questioned its sensitivity as a diagnostic tool for SPPV and GTPV. For example, Rhazi *et al.* (2022) compared the sensitivity of the commercially available ID-Vet ELISA with SPPV VNT performed using primary lamb testis cells or embryonic sheep skin (ESH-L)/ovine testis cell lines. Results from 220 field samples collected from sheep showed that the ELISA failed to detect approximately one in five positive samples, whereas the ESH-L cell line performed best for VNT; moreover, the assay could be coupled with immunoperoxidase staining to provide a quantitative readout (Rhazi *et al.*, 2022). These findings confirmed earlier observations regarding the sensitivity of ESH-L cells for CaPV growth and detection (Rhazi *et al.*, 2021a).

However, several studies have highlighted the potential utility of novel ELISA platforms. Recently, Reddy *et al.* (2025) developed an indirect ELISA using recombinant A27L derived from the Romanian strain of SPPV as the diagnostic antigen. Compared with VNT, the assay demonstrated diagnostic specificity of 96% and 98% and sensitivity of 98% and 97% when tested using sera from sheep and goats, respectively (Reddy *et al.*, 2025b). Similarly, the competitive CaPV ELISA developed by Baselli *et al.* (2023) detected GTPV seroconversion in goats earlier and with 100% specificity compared with the ID-Vet ELISA and VNT, while also performing well with sera from sheep infected with SPPV (Baselli *et al.*, 2023).

Madhavan *et al.* (2023) used E. coli-expressed CaPV ORF095 and ORF103 proteins as diagnostic antigens in an ELISA, demonstrating sensitivity and specificity for antibodies against SPPV and GTPV, with ORF095 ultimately performing better when tested with field sera (Madhavan *et al.*, 2023).

Dashprakash *et al.* also used E. coli expression systems, this time to produce the GTPV ORF117 gene product. The purified recombinant A27 protein was subsequently used as a diagnostic antigen in an indirect ELISA, where it demonstrated diagnostic specificity of 88.7% and sensitivity of 98.5% across 500 serum samples (Dashprakash *et al.*, 2019). Similarly, an E. coli-expressed recombinant partial P32 protein used in ELISA demonstrated diagnostic specificity of 100% and sensitivity of 97.1% relative to a whole-virus-antigen-based ELISA when tested using sera from SPPV-infected sheep or GTPV-infected goats (Venkatesan *et al.*, 2018).

Kushwaha *et al.* (2024) explored the use of baculovirus-expressed GTPV core (A4L and A12L) and EEV (A33R) proteins as diagnostic antigens in ELISA, ultimately selecting the A33R-based assay for further optimisation. The final ELISA demonstrated diagnostic sensitivity and specificity of 89% and 94% in goats and 98% and 91% in sheep, respectively, using sera from infected, vaccinated, and uninfected animals (Kushwaha *et al.*, 2024).

Together, these studies represent promising progress towards practical, safe, and accurate tools for serological monitoring of SPPV and GTPV in settings where VNT is not the preferred option.

See also (Berguido *et al.*, 2022; Teffera *et al.*, 2026), described in the LSDV diagnostics section, (ELISA sub-section).

Immunoperoxidase monolayer assay

The use of immunoperoxidase monolayer assays for the diagnosis of SPPV or GTPV has been discussed by Haegeman *et al.* in their 2020 publication. While the primary aim was LSDV detection, the authors showed that the assay could be easily modified to detect SPPV or GTPV, and was able to detect specific antibodies earlier in approximately one half to three quarters of animals, and performed with comparable diagnostic sensitivity and specificity to VNT (Haegeman *et al.*, 2020).

Luminex

See (Berguido *et al.*, 2024b), described in the LSDV diagnostics section, (Luminex sub-section).

Laser-induced graphene (LIG)-based electrochemical immunoassay

To our knowledge, no studies have yet reported the application of LIG to the diagnosis of SPPV or GTPV.

Machine learning

To our knowledge, no studies have yet reported the application of machine learning approaches to the diagnosis of SPPV or GTPV.

Differentiating infected from vaccinated animals (DIVA)

Genetic DIVA

Unlike LSDV, there are currently no commercially available DIVA real-time PCR assays for SPPV or GTPV. Research efforts have therefore focused on developing novel approaches to distinguish animals infected with field strains from those vaccinated with attenuated virus strains.

Genetic DIVA is an important tool for understanding the cause of disease or disease-like symptoms, which may arise from virulent infection, vaccination with attenuated virus, or poorly controlled vaccine-related revertant strains. In 2018, Chibssa *et al.* identified an 84-nucleotide deletion present in Romanian and Yugoslavian RM/65 vaccine strains but absent from African and Asian SPPV field strains. The researchers subsequently developed and tested a gel-based PCR assay targeting this region, which distinguished SPPV field and vaccine strains with limits of detection of 80 and 10 copies per reaction, respectively, and 100% specificity (Chibssa *et al.*, 2018).

See also (Wolff *et al.*, 2021a) in the LSDV diagnostics subsection (Genetic DIVA sub-section).

Serological DIVA

See (Berguido *et al.*, 2023) in the LSDV diagnostics subsection (Serological DIVA sub-section).

Sampling strategies and other developments

See (Das *et al.*, 2024) in the LSDV diagnostics subsection (Sampling strategies and other developments sub-section).

Pathogenesis

In addition to the obvious clinical symptoms (skin lesions, lethargy, etc.), SPPV infection in sheep has also been associated with dysregulated serum mineral concentrations and altered levels of circulating cytokines, liver enzymes, urea,

malondialdehyde, and other critical metabolites (Bozukluhan *et al.*, 2018; Karademir, 2021; Karakurt *et al.*, 2023a, 2023b; Kirmizigul *et al.*, 2016). Caspase expression appears to be suppressed within SPP lesions, indicating viral anti-apoptotic activity (Haligur and Ozmen, 2016). Mortality associated with SPPV and GTPV outbreaks is known to vary widely, but the molecular determinants of disease severity remain unclear. Single-nucleotide polymorphisms in host immune and antioxidant genes have been associated with disease status, although the causative and mechanistic implications of these findings remain unknown (Darwish *et al.*, 2025a).

***In vivo* studies**

Xin *et al.* characterised the GTPV N1L gene, which belongs to a known family of poxvirus virulence factors, by cloning it into a recombinant VACV and comparing it with wild-type virus (Xin *et al.*, 2025). *In vivo* assessment in mice indicated significantly higher replication and toxicity in the recombinant virus expressing GTPV N1L, with an overall 7.5-fold increase in virulence compared with wild-type VACV. The researchers attributed this difference to greater effects on vascular endothelial cells and enhanced ability of the recombinant virus to cross the blood–brain barrier (Xin *et al.*, 2025).

Researchers in Saudi Arabia studied samples from 50 Barki ewes naturally infected with SPPV in the field alongside 50 healthy controls, aiming to identify genetic, immunological, and biochemical markers associated with susceptibility. The researchers found that SPPV-infected sheep exhibited microcytic hypochromic anaemia and leucocytosis, together with higher levels of proinflammatory cytokines and lower IL-10 concentrations compared with controls. Infection was also associated with increased acute phase proteins, oxidative stress markers, and cortisol levels in blood, accompanied by reduced antioxidant capacity and transferrin concentrations (Darwish *et al.*, 2025a).

Wolff *et al.* established a challenge model for SPPV infection via intravenous, intranasal, and contact transmission routes, validating pathogenesis and clinical presentation using Indian and Egyptian isolates (Wolff *et al.*, 2020a). Finally, Sudriyal *et al.* conducted a spatiotemporal study of infection by the virulent GTPV Mukteshwar strain in seronegative goats, providing an in-depth analysis of viral pathogenesis and identifying benchmarks to assist in determining vaccine efficacy (Sundriyal *et al.*, 2026).

***In vitro* studies**

A transcriptomic study of lamb testis cells infected with SPPV identified modulation of numerous genes involved in viral attachment and cell entry, cellular immune responses, early viral protein expression, and inhibition of apoptosis (Sonowal *et al.*, 2021). A later analysis of differentially expressed genes and protein–protein interaction networks by the same research group identified highly connected protein hubs (e.g., AURKA and MAPK14) and enriched signalling pathways downstream of the TP53 master regulator (Sonowal *et al.*, 2022).

Exosomes secreted by SPPV-infected sheep testis cells are known to contain altered levels of various miRNAs compared with control cells (He *et al.*, 2019). Ma *et al.* conducted a bioinformatics analysis of these miRNAs, identifying several differentially expressed miRNAs primarily associated with the Arf6 downstream pathway (Ma *et al.*, 2024). This group also found that SPPV infection modulated expression of the miRNA miR-29a, which was able to reverse the reduced growth rate and increased apoptosis characteristic of SPPV infection (Ding *et al.*, 2024).

Alwan *et al.* assessed the envelope proteins of Iranian SPPV and GTPV variants responsible for higher-severity outbreaks, identifying mutations in the P32 gene associated with enhanced binding to the cognate proteoglycan receptor of the P32 protein (Alwan *et al.*, 2023).

In light of CaPV–PPRV co-infections observed in the field (Akanbi *et al.*, 2020), Kuniyal *et al.* analysed co-infection kinetics between GTPV and PPRV in Vero cells (Kuniyal *et al.*, 2022). Both viruses were able to coexist within the same cells at low multiplicity of infection, whereas at high multiplicity, PPRV was excluded by GTPV (Kuniyal *et al.*, 2022).

Finally, Long *et al.* recently characterised the GTPV protein Hrf-063, which was found to interact with host eukaryotic translation initiation factor 4A1 (eIF4A1) in pull-down and co-immunoprecipitation studies (Long *et al.*, 2026). Functional analyses indicated that the interaction between these two proteins during infection affects a variety of host immunological mediators including STAT1, ISG15, and STING1, and modulation of the Hrf-063-eIF4A1 axis altered the expression of viral virulence-associated proteins and infectious virion production (Long *et al.*, 2026).

Immunology

Similarly to LSDV infection, animals that survive natural infection with virulent GTPV or SPPV are believed to develop lifelong immunity. It is often stated in the literature that cell-mediated immunity is the dominant protective mechanism, yet studies clearly defining the nature of the protective immunological memory that follows infection, or the factors driving its development, remain limited. Several studies report worthwhile advances in knowledge, although much remains to be understood.

Immunogenetics

The WOAH states that native breeds of goats and sheep in disease-endemic areas are far less susceptible to SPPV- and GTPV-associated morbidity and mortality than non-native breeds, particularly those of European or Australian origin (WOAH, 2013), although the reasons for this remain unclear.

In addition, field observations suggest inter-individual variation in susceptibility within breeds. One study attempted to shed light on this phenomenon: Darwish *et al.* (2025) identified 23 single-nucleotide polymorphisms between Barki ewes that were infected with SPPV in the field and those that remained uninfected. The ewes originated from the same farm and were co-housed during the study period; thus, animals that did not succumb to infection were considered less susceptible to disease. Among the polymorphisms were several non-synonymous variants, including in genes encoding IL-1β, IFN-γ, and the antioxidant enzymes PRDX2 and Nrf2, which showed possible, although as yet unconfirmed, associations with disease susceptibility (Darwish *et al.*, 2025a).

Although not without limitations (as acknowledged by the researchers), this study represents a much-needed shift in focus towards understanding the factors underpinning natural resistance, which may ultimately help inform the development of improved therapeutics and vaccines.

Innate immunity

Several studies have begun to dissect the key molecular players involved during early infection with GTPV or SPPV *in vivo, ex vivo*, and *in vitro*.

Zeng *et al.* (2016) experimentally infected goats with the GTPV FZ strain and collected blood samples daily for 6 days before euthanising and necropsying the animals. This revealed that type I IFN transcripts increased in peripheral blood lymphocytes from 12–24 h post-infection, and that the early response in these cells also involved increased transcription of genes encoding suppressor of cytokine signalling-1, IL-1β, IL-6, IL-18, and TNF-α (Zeng *et al.*, 2016). The same transcripts were also expressed in lung and spleen tissues on day 6, together with genes encoding several ISGs and TLR2 and TLR9 (Zeng *et al.*, 2016).

Building on earlier work showing the susceptibility of immune cells to SPPV infection in lambs *in vivo* (Gulbahar *et al.*, 2006), Chibssa *et al.* (2021) exposed PBMCs *ex vivo* to virulent and attenuated SPPV and compared expression of key immune molecules with control cells (Chibssa *et al.*, 2021a). This approach revealed high expression of the pattern-recognition receptor RIG-I in SPPV-exposed PBMCs, while viral exposure was also associated with production of TNF-α, IL-15, and IL-10 (Chibssa *et al.*, 2021a).

He *et al.* (2019) explored the potential role of exosomes, nanosized intercellular communication vesicles, in shaping the immune response to SPPV. The researchers infected primary ovine testicular cells with a low-passage field isolate of SPPV and analysed the exosomes and exosomal miRNAs produced. They identified potential target genes within the mTOR

and MAPK signalling and autophagy pathways, both of which are important for antiviral immune defence (He *et al.*, 2019).

Adaptive immunity

One study reported peripheral and tissue cytokine responses during natural SPPV infection; Karakurt *et al.* (2023) used post-mortem skin, lung, and kidney samples to identify the cytokine transcripts predominating locally during natural infection. In skin, SPPV-positive cells in the dermis labelled most strongly for TNF-α and IFN-γ, but also for IL-1β, IL-2, IL-6, IL-8, IL-10, and IL-12. In the lung, bronchial and bronchiolar epithelial cells and alveolar macrophages similarly expressed these cytokines, as did infiltrating mononuclear inflammatory cells. In the kidney, cytokine expression was primarily detected in non-purulent interstitial nephritis foci and degenerated tubular epithelial cells (Karakurt *et al.*, 2023b). The researchers noted that most infected cells were monocytes, macrophages, and some fibroblasts.

Immune evasion

One study in 2018 reported the immune-modulatory role of GTPV ORF135, which inhibited Nf-κB pathway activation and apoptosis in HEK-293T cells *in vitro* and was required for full virulence in sheep *in vivo* (Zhang *et al.*, 2018). Insights gained from studies of LSDV, as discussed in the LSDV Immune evasion section above, may also prove relevant.

Control of the disease

CaPV DNA is known to persist in the environment, facilitating relatively simple and low-tech sample collection methods to supplement surveillance programmes (Brown *et al.*, 2024). Villalba & Haegeman *et al.* also reported that non-infectious SPPV genomic DNA could be detected in oral swabs months after post-outbreak cleaning and disinfection, likely as a result of environmental contamination; PCR analysis of sentinel animals during post-outbreak repopulation should therefore be interpreted with caution (Villalba *et al.*, 2024).

In Spain, control of the 2022–2023 SPP outbreaks centred on EU legislation, including complete culling of affected herds, zoning and animal movement restrictions, and heightened biosecurity and passive surveillance (Germán *et al.*, 2024). Among the various control measures implemented, Germán *et al.* highlighted awareness campaigns targeting farmers and veterinarians, farm and animal transport biosecurity, strict animal movement control, and adaptive sizing and timing of restricted zones as particularly important for limiting the spread of SPPV (Germán *et al.*, 2024).

Rawlins *et al.* recently described development of a mobile app, SR-DISVAXFIC, designed to estimate herd-level costs and vaccination benefits for small ruminant diseases such as SPP and GTP in field settings (Rawlins *et al.*, 2026). The app was field-tested by veterinarians in northern Nigeria on sedentary and transhumance herds that had experienced SPP and GTP outbreaks. Results indicated positive benefit/cost ratios for vaccination (7:1 for sedentary herds and 4.28:1 for transhumance herds), regardless of the level of government subsidisation, while real-time parameter input via the app produced narrower confidence intervals for economic estimates compared with earlier stochastic modelling approaches (Rawlins *et al.*, 2022). The researchers noted that co-infections may lead to some overestimation of benefit (Rawlins *et al.*, 2026). Bardhan *et al.* similarly reported a highly positive benefit/cost ratio for GTP vaccination in India (19:1) (Bardhan *et al.*, 2020).

As with LSD, participatory epidemiology has shown considerable promise for harmonising large-scale SPP/GTP surveillance and research with the needs and priorities of local and regional stakeholders, while also identifying transmission-associated risk factors in remote areas (Alemayehu *et al.*, 2015; Mpouam *et al.*, 2021). These approaches provide valuable opportunities for data collection, animal health monitoring, and disease control prioritisation in less accessible and resource-limited regions, enabling researchers to better understand the socioeconomic realities faced by small ruminant farmers and to begin mapping animal movement networks, treatment practices, and their relationships with poxvirus prevalence and persistence (Bagdi *et al.*, 2016; Yadav *et al.*, 2018). Participatory methods may be particularly useful in regions such as sub-Saharan Africa, where information on disease prevalence is often distributed among local stakeholders rather than centralised through laboratory and surveillance systems (Abdilatif *et al.*, 2018; Adwok *et al.*, 2018; Moenga *et al.*, 2016; Mpouam *et al.*, 2021; Nantima *et al.*, 2018). It is also critical that small ruminant farmers and veterinarians in currently disease-free regions are able to differentiate SPP and GTP from other endemic diseases with similar clinical presentations (Simpson *et al.*, 2023).

Anticipating that other CaPVs may follow the outward spread of LSD from traditionally endemic regions of Asia and Africa, Chibssa *et al.* developed an alignment-free approach for discriminating African, Western/Central Asian, and Eastern/Southern Asian GTPV strains based on viral GPCR sequences (Chibssa *et al.*, 2021b). This method may help identify specific international transmission networks in the event of SPPV or GTPV incursions into Europe.

Policy

As with other highly contagious animal pathogens, control measures for SPP/GTP outbreaks in non-endemic areas typically centre on extensive culling of infected and exposed herds, restrictions on animal movement to and from affected areas, and cleaning/disinfection of farms and associated equipment (EFSA Panel on Animal Health and Welfare (AHAW) *et al.*, 2021; Papadimas, 2025). SPP and GTP were included in European Law 2016/429, which was intended to eliminate the need for a patchwork of bilateral animal trade agreements by harmonizing animal health regulations across the EU

(Loria *et al.*, 2020). This regulation remains in effect across the EU (Loria *et al.*, 2022) and, with some minor amendments, in the UK (Benyon, 2023). An assessment of European control measures for SPP and GTP estimated that establishment of a protection zone of 5.3 km around an infected area would provide a 95% probability of containing transmission, rising to 99% at 19.4 km (EFSA Panel on Animal Health and Welfare (AHAW) *et al.*, 2021).

In the United States, SPP and GTP are classified as animal select agents capable of causing severe harm to animal health and safety, requiring enhanced oversight and imposing restrictions on the movement and use of these viruses for research (Pillai *et al.*, 2023).

Participatory epidemiology can play a major role in policy by identifying regions in which animal movement is particularly common or extensive. Ijoma *et al.* combined market surveys with participatory approaches to map small ruminant movement in northern Nigeria, identifying interstate mobility networks and "super-spreader" regions particularly likely to sustain virus circulation (Ijoma *et al.*, 2025). Such studies may help target policy, surveillance, and limited disease control resources to regions where they can achieve the greatest benefit-to-cost ratio.

Therapeutics

Veterinarians generally focus on treatment of secondary bacterial infections (Pothiappan *et al.*, 2018) or prophylactic antibiotic administration in animals suspected of having GTPV/SPPV infection (Malmarugan *et al.*, 2015).

Silver nanoparticles have been shown to inhibit GTPV replication *in vitro* by preventing viral entry into host cells (Saadh, 2023).

Vaccines

Several LAVs against SPPV/GTPV are commercially available, including locally produced options; together, their performance varies from good to poor, and new studies have shed light on some of the reasons for this. Researchers have also attempted – with varying success - to achieve the same efficacy using experimental inactivated vaccines. Advances across these vaccine types and others are reported below.

Homologous LAVs

Homologous LAVS against SPPV/GTPV are widely stated to provide long-lived immunity, though annual booster immunisations are recommended. In reality, efficacy in the field seems to occur within a wide range and there are reports of outbreaks in the presence of vaccine usage, for example in Algeria (Kali *et al.*, 2019) and – in the case of GTPV at least

– extreme pathologies in some breeds in response to current LAVs. At present, there are not any DIVA-enabled LAVs against these pathogens.

Licensed homologous LAVs

The complete characterisation of vaccine strains is an important and ongoing task. Since 2015, the genome sequences for the Gorgan GTPV strain from the Jordanian Caprivac vaccine (Mathijs *et al.*, 2016a) and the SPPV-Srin38/00 strain from India, which was attenuated through serial passage in lamb testis cells followed by Vero cells (Kumar *et al.*, 2022), have both been published.

The majority of studies report animal trials to assess vaccine efficacy. Shumilova *et al.* (2025) tested four commercially available SPPV vaccines (RM65, KSGP 0240, KSGP ARRIAH, and NISKHI ARRIAH) against a cluster 1.1 virulent field strain isolated in Russia in 2023. All vaccines were well tolerated, and all except KSGP 0240 elicited high neutralizing antibody titres by day 21 post-immunisation (Shumilova *et al.*, 2025). Although the NISKHI ARRIAH vaccine induced the highest antibody titres, all vaccinated groups exhibited comparable levels of clinical protection and were negative by real-time PCR following challenge, including animals vaccinated with KSGP 0240 (Shumilova *et al.*, 2025). In addition to providing useful practical information, this study highlights the need for further investigation into correlates of vaccine-induced protection beyond neutralising antibody titres.

While such studies are indeed useful, their results may only be fully applicable to the exact setting in which they were tested. For example, while Hamdi *et al.* (2020) reported that sheep vaccinated with the Romania SPPV vaccine were fully protected from virulent challenge 28 days later(Hamdi *et al.*, 2020a), the same vaccine strain performed poorly under field conditions in Egypt in 2018–2019 (Oreiby *et al.*, 2022). In the latter setting, the RM-65 vaccine protected sheep effectively, whereas following use of the Romania vaccine, almost 80% of immunised sheep developed mild clinical signs and more than 35% died during infection (Oreiby *et al.*, 2022).

Another factor that could shape vaccine efficacy and/or side-effects is the administration of dietary supplements at the time of vaccination (or presumably the basal levels of these nutrients in animals' diets). Darwish *et al.* (2024) found that administration of vitamin E and selenium (but not BCG or levamisole) to Barki ewes immediately before immunisation with an SPPV LAV significantly reduced vaccination-associated side effects and enhanced humoral responses (Darwish *et al.*, 2024), although protection following challenge was not assessed. The same group also showed that 5 days of oral supplementation with oregano- or artichoke- extract-based formulations following vaccination mitigated adverse effects associated with SPPV LAV (Darwish *et al.*, 2025b) immunization.

Interesting work has also been done on immune responses to GTPV LAVs. In an unusually long-term study, Bhanuprakash *et al.* (2022) immunised goats with a single dose of a locally produced GTPV/Uttarkashi/1978 LAV and monitored immune

responses and protective efficacy against a culture-adapted virulent strain for more than 4 years. Specific antibody levels peaked 21 days post-immunisation before declining, although they remained detectable for 1–2 years. Despite reduced serum neutralisation titres over time, animals remained protected from clinical disease throughout the study period, although viral shedding was not assessed (Bhanuprakash *et al.*, 2022). These findings confirmed earlier work on a GTPV LAV, which additionally showed that antibody levels reached protective thresholds within 7 days post-immunisation (Baksi *et al.*, 2017).

A similar long-term field study of sheep in Mongolia vaccinated with a locally produced LAV reported substantial inter-animal variability in antibody responses, with some sheep testing negative by ELISA after 40 days, whereas others maintained detectable antibody levels for almost 9 months post-immunization (P. Fay *et al.*, 2022). Although protection was not assessed, the study demonstrated the practical utility of the ID-Vet ELISA for serological monitoring, showing good correlation with serum neutralization titres while offering advantages in cost and feasibility for resource-limited settings.

In summary, while some progress has been made, there is much that we do not yet understand about how to apply the available LAVs against SPPV and GTPV in the field to achieve maximum efficacy across the full range of settings, while minimising side-effects.

Novel homologous LAVs

Several attempts to generate new and improved live attenuated SPPV/GTPV vaccines have been reported.

One way of improving existing vaccines is via modifying the means or efficacy of antigen delivery. Al-Zubaidi and colleagues formulated chitosan nanoparticles as a novel mucosal delivery system for an SPPV LAV, which exhibited favourable encapsulation and release characteristics in *vitro* (Al-Zubaidi *et al.*, 2023). If effective *in vivo*, such a system could offer several advantages, including ease of administration and induction of stronger mucosal immunity. Earlier work also explored the use of chitosan nanoparticles in injectable SPPV vaccine formulations; although animal numbers were small, there was some evidence that sheep receiving the chitosan-containing vaccine generated peak antibody titres approximately 1 week earlier and maintained detectable responses for longer (Mohamed *et al.*, 2017).

See also (Biswas *et al.*, 2019) in the LSDV vaccines section, (Licensed homologous LAVs sub-section).

Maternal immunity

A single study aimed to define the optimal timing for first administration of a GTPV vaccine to kids born to does vaccinated 6 months before parturition. The researchers found that two of the ten kids tested had lost seropositivity (measured by virus neutralisation test) by day 56, while all animals became seronegative between 100 and 120 days after

birth (Abdollahi *et al.*, 2024). In sheep, vaccine-induced maternal antibodies protected lambs for up to 60 days after birth (Ebrahimi-Jam *et al.*, 2022)

Adverse events relating to current homologous LAVs

Relative to the well-characterised "Neethling response" following LSDV LAV administration, much less is known about the side-effect profile of SPPV/GTPV LAVs. Recent studies have begun to shed light on some parallels and key differences, especially those relating to inter-breed variation.

As observed in a study of cattle immunised with an SPPV/GTPV LAV in Russia (Burkov *et al.*, 2021), Darwish *et al.* (2022) also reported notable increases in blood markers of oxidative and hepatic stress in Barki sheep during the 2 weeks following immunisation with a locally produced SPPV LAV (Darwish *et al.*, 2023).

Meanwhile a notable study in goats compared vaccine-associated adverse effects among Saanen, Alpine, Murcia-Granada, Saanen-Mahabadi, and Alpine-Mahabadi breeds following vaccination with a locally produced Gorgan strain LAV (Ghorani and Esmaeili, 2022). The researchers reported a striking susceptibility of imported European Saanen goats, with 90% of animals (n=82) developing skin lesions and 27% dying, while 27% of European Alpine goats developed skin lesions and 10% died following vaccination (Ghorani and Esmaeili, 2022). Animals that were crosses between European and Iranian breeds tolerated vaccination more successfully and were similarly protected against virulent challenge. The same group subsequently sought to define an optimal immunisation strategy for Saanen goats and found that one or two prior immunizations with an inactivated vaccine then enabled animals to tolerate the LAV while developing long-lasting protective immunity (Esmaeili *et al.*, 2025). Such studies represent a commendable solution-focused approach to problems seen in the field, with immediately actionable findings of real use to farmers in the region; they also call for more thorough investigation of the basis for breed-specific differences and highlight the need for vaccine manufacturers to consider different genetic backgrounds when testing their products.

Alongside breed susceptibility, adverse effects associated with GTPV LAVs may also be dose dependent. Pregnant non-native Murcia-Granada goats in Iran receiving twice the standard vaccine dose exhibited abortion rates approaching 40%, together with fever and lesions attributable to infection with the vaccine strain, whereas the standard dose was well tolerated (Esmaeili *et al.*, 2024). These findings highlight the importance of tailoring vaccination strategies to breed, life stage, and regional context to avoid adverse outcomes.

As seen for LSDV, there remains a need for improving vaccine testing and quality control, especially for locally produced LAVs. Kali *et al.* (2019) reported poor protection associated with the locally produced RM/65-based LAV used in Algeria, which the researchers attributed to low immunogenicity and/or inadequate quality control (Kali *et al.*, 2019). Notably, an LAV based on this strain (manufacturer unspecified) performed well during an outbreak in Egypt in 2018–2019,

whereas use of the Romania vaccine resulted in almost 80% of immunised sheep developing mild clinical signs and more than 35% dying following infection (Oreiby *et al.*, 2022).

Poor quality control can also have consequences beyond lack of protection from the intended pathogen. Bumbarov *et al.* (2016) identified BTV mRNA in commercially available SPPV and LSDV vaccine batches (Bumbarov *et al.*, 2016), and later that same year, SPPV vaccine-associated BTV was shown to have spread through Tunisia (Lorusso *et al.*, 2018).

Heterologous LAVs

Though heterologous vaccination is less-commonly utilised for SPPV or GTPV, a handful of studies report the results of LSDV vaccination of sheep or goats, or of the use of an SPPV or GTPV vaccine to protect against the heterologous pathogen.

Licensed heterologous LAVs

Hamdi *et al.* reported that only one quarter of sheep vaccinated with a Neethling-based LSDV vaccine seroconverted, while only half were protected from SPPV challenge at 28 days post-immunization. By contrast, five of eight goats vaccinated with a Romania SPPV LAV seroconverted, and none developed clinical signs following challenge with virulent GTPV (Hamdi *et al.*, 2020a). Similarly, Berguido *et al.* reported that sera from goats vaccinated against GTPV were capable of cross-neutralising SPPV *in vitro* (Berguido *et al.*, 2024a).

Previously, Boshra and colleagues (2015) showed that a Kenyan SPPV/GTPV vaccine which is based on LSDV with an IL-10 homologue gene deleted, protected both sheep and goats against virulent SPPV/GTPV challenge, respectively (Boshra *et al.*, 2015b).

See also (Shoulah *et al.*, 2022) in the LSDV vaccines section, (Licensed heterologous LAVs sub-section).

Novel heterologous LAVs

We did not find any reports of novel heterologous LAVs targeting SPPV or GTPV.

Adverse events relating to current heterologous LAVs

We did not find any reports within this section.

Inactivated vaccines

Inactivated vaccines remain an attractive option through their increased safety profile, and two studies reported the possible advantage of an improved humoral response compared to homologous or heterologous LAVs.

Most recently, Wolff *et al.* compared the protective efficacy in sheep of two doses of a novel BEI-inactivated LSDV vaccine (based on a Serbian field strain) with a single dose of the commercially available Neethling-based Lumpyvax® vaccine (Wolff *et al.*, 2023). Three weeks after the final immunisation, sheep were challenged with the SPPV-India/2013/Surankote strain. Both vaccines were well tolerated and effective in protecting against clinical disease but did not prevent viral shedding in nasal fluid. However, the inactivated vaccine elicited earlier and stronger humoral immune responses than Lumpyvax® (Wolff *et al.*, 2023).

Another promising study earlier reported similar findings. Boumart *et al.* (2016) compared the immunogenicity and protective efficacy of two immunisations with a β-propiolactone-inactivated Romanian SPPV vaccine against a single immunisation with a Romanian SPPV LAV. The researchers found that the inactivated vaccine was well tolerated and elicited more sustained neutralising antibody responses than the LAV, with titres persisting to the end of the experiment at nine months post-immunisation. Moreover, the inactivated vaccine provided comparable clinical protection and reduction in viral shedding to the LAV (Boumart *et al.*, 2016).

These studies show that inactivated vaccines may yet have great potential, however the disadvantage to farmers of needing two immunisations compared to one is significant. Future studies might explore dose titration, adjuvant usage and inactivated/LAV combination regimes.

Subunit vaccines

Subunit vaccines represent an attractive option for non-endemic countries wishing to incorporate vaccination into disease control strategies, as they may more readily support DIVA and are generally safer to produce than LAVs. However, protective antigens for SPPV and GTPV, as for LSDV, remain incompletely defined, and the novel vaccines reported below have yet to be tested in natural host species *in vivo*.

Researchers working in China recently reported the computational design of an MEV against GTPV comprising predicted T- and B-cell epitopes within the P32, L1R, and ORF095 proteins (Long *et al.*, 2024). The resulting construct was predicted to be soluble, non-toxic, to stably bind TLR2, TLR3, and TLR4, and to exhibit strong immunogenicity (Long *et al.*, 2024).

Chervyakova *et al.* (2016) evaluated the immunogenicity of several SPPV structural proteins in rabbits, reporting that SPPV-ORF060, SPPV-ORF117, and SPPV-ORF122 elicited sera capable of neutralising SPPV *in vitro*, whereas SPPV-ORF095 did not (Chervyakova *et al.*, 2016).

See also (Teffera *et al.*, 2025) in the LSDV vaccines section, (Subunit vaccines sub-section).

Multi-valent vaccines

The advantages of multi-valent vaccines are clear, especially in resource-low settings. However, as revealed by the studies below, while some formulations retain efficacy across all pathogens, others demonstrate the risk of immunological interference.

One way of creating multi-valent vaccines is to use one of the pathogens as both an immunogen in its own right and as a vector for antigens from other pathogens. Boshra *et al.* achieved this using their rationally attenuated LSDV LAV that was engineered to lack ORF005, which encodes an IL-10 homologue (Boshra *et al.*, 2015b), as an immunogenic vector for a heterologous GTPV/SPPV vaccine; they then incorporated protective antigens against PPRV and Rift Valley fever virus to generate a multi-valent vaccine (Boshra *et al.*, 2024).

Researchers in China similarly developed a recombinant AV41 GTPV expressing the EG95 antigen from Echinococcus granulosus (the causative agent of cystic hydatidosis) and confirmed correct expression of the foreign antigen *in vitro* (Liu *et al.*, 2018). However, the efficacy of this bivalent vaccine *in vivo* remains to be established. The same group subsequently refined this approach by removing marker genes present in the original recombinant GTPV and demonstrating stable antigen expression (Liu *et al.*, 2019).

Although combined PPRV and SPPV vaccines are well-established, in 2021, Amanova *et al.* developed a combined PPRV-SPPV vaccine based on the Nigeria 75/1 and NISKHI strains, respectively. This vaccine elicited protective immunity against both pathogens in Kazakh breed sheep for the full 12-month duration of the study, despite a progressive decline in SPPV-neutralising antibody titres from six months post-vaccination (Amanova *et al.*, 2021). The NISKHI SPPV strain was also used as a vector for the FMDV VP1 and Brucella spp. outer membrane proteins by Chervyakova *et al.* (2021), who reported successful antigen expression *in vitro* and immunogenicity in mice (Chervyakova *et al.*, 2021)

In 2015, Fakri *et al.* evaluated a bivalent LAV comprising the Nigeria 75 strain of PPRV and the Romania strain of SPPV in sheep and goats and compared its protective efficacy with that of the monovalent SPPV vaccine in sheep challenged with the local MOR1998 SPPV strain. The researchers reported that the bivalent vaccine was well tolerated under laboratory conditions, elicited antibody responses in sheep comparable to those induced by the monovalent vaccine, and provided equivalent protection against challenge (Fakri *et al.*, 2015). In subsequent field trials, approximately 90% of immunised sheep seroconverted by day 21, although long-term protection was not assessed (Fakri *et al.*, 2015).

While the studies above report successful multi-valency, other researchers report immunological interference especially in the case of vaccine co-administration. For example, sheep immunised with a combination of locally produced PPRV (Nigeria 75/1 strain) and GTPV vaccine (undisclosed strain) developed lower neutralising antibody responses to GTPV but higher responses to PPRV compared with single immunisation using the same vaccines (Zhang *et al.*, 2021). The

researchers also examined cellular co-infection with the two viruses *in vitro* and confirmed that the infections interfered with each other, urging caution regarding co-immunisation strategies.

Similarly, Hurisa *et al.* (2024) showed that simultaneous administration of vaccines against PPRV, contagious caprine pleuropneumonia, pasteurellosis, and SPPV/GTPV in goats resulted in non-seroconversion to GTPV/SPPV despite strong responses to the other pathogens; by contrast, animals vaccinated singly developed robust humoral responses (Hurisa *et al.*, 2024). This study highlights the importance of carefully evaluating the effects of increasing vaccine valency on immune responses to individual pathogens, while also supporting the rationale for multivalent vaccines containing a limited number of protective epitopes rather than simultaneous administration of multiple independent vaccines.

Complicating the issue further, there is a single report of combined immunisation improving responses to one of the pathogens. Researchers in Egypt reported protection of sheep against challenge with either PPRV or SPPV following a single immunisation with a combined freeze-dried LAV comprising both pathogens (Saad *et al.*, 2024). Interestingly, co-administration in this case resulted in higher antibody titres against PPRV while not affecting antibody responses to SPPV compared with groups immunised with the corresponding monovalent vaccines (Saad *et al.*, 2024).

See also (Tareq *et al.*, 2025) in the LSDV vaccines section, (Multivalent vaccines sub-section).

Vectored vaccines

We did not find any reports of novel vectored vaccines targeting GTPV or SPPV.

DIVA-enabled vaccines

We did not find any reports of novel DIVA-enabled vaccines targeting GTPV or SPPV.

Vaccine production

Several studies have reported new or improved ways of producing SPPV/GTPV vaccines.

Uzar & Turan (2022) showed that MDBK cells could be used for propagation of the SPPV Bakırköy vaccine strain (Uzar and Turan, 2022). More recently, the same group showed that Vero cells could support scalable microcarrier-based culture of the same strain, achieving approximately threefold higher viral titres compared to conventional monolayer approaches (Çolak *et al.*, 2025). A similar strategy had previously been successfully applied to the RM65 SPPV strain (Trabelsi *et al.*, 2014).

In 2020, researchers in Russia sought to define suitable cell lines and culture conditions for streamlined local vaccine production against SPPV, GTPV, PPRV, BTV, and orf virus. Balyshev *et al.* evaluated sheep kidney (PO-VNIIVViM) and saiga kidney (PS-VNIIVViM) cell lines and demonstrated that both supported high-titre production of SPPV (strain B-5/96) and GTPV (strain OK/A-04) vaccine strains in roller bottle cultures (Balyshev *et al.*, 2020)

A research group in Kazakhstan has also completed a series of studies exploring plant-based production of SPPV proteins for potential use in subunit vaccines. Following a proof-of-principle study in 2016 (Beisenov *et al.*, 2016), the researchers reported expression of the SPPV structural proteins A27L and L1R in *Nicotiana tabacum* chloroplasts, achieving yields of 1–2% of total soluble protein (Stanbekova *et al.*, 2018). In 2020, they refined this approach and successfully produced and purified a truncated form of L1R (Beisenov *et al.*, 2020). Subsequently, in 2021, they showed that the same method could be applied to the SPPV117 structural protein, which was purified and recognised by sera from SPPV-infected sheep (Stanbekova *et al.*, 2021). Results from *in vivo* testing remain awaited.

Conclusions

Morbidity and mortality due to SPP and GTP are major sources of economic hardship for the many populations in endemic areas that depend on small ruminant farming for their livelihoods and welfare. As with LSD, the limited economic resources available in many of these endemic areas hamper our ability to monitor and control the spread of SPP and GTP. The recent SPP outbreaks in Spain, occurring ~50 years after its original eradication, serve as a reminder that anthropogenic animal movements can facilitate unexpected disease transmission events over long distances.

The studies discussed above represent some of the strides made over the past decade in our understanding of SPPV and GTPV, their biology and epidemiology, host-pathogen interactions, and control measures. Substantial progress has been made, but many questions remain to be answered (see Future research priorities below). Like LSD, many of the biggest barriers to effective control of SPP and GTP are primarily economic. The low- and middle-income countries that currently take the brunt of economic losses from these diseases also face a lack of well-trained and experienced veterinarians (and/or ability to access these veterinary services). Rural regions may also be unable to access laboratory facilities necessary for effective disease diagnosis and surveillance programmes, and the cold chains necessary for vaccine transport may also be unable to reach these areas. For instance, a study in Tanzania on factors affecting decision to vaccinate small ruminants found that “improving the knowledge of livestock owners regarding the priority diseases and the benefits of vaccination, establishing more vaccine suppliers, improving vaccine distribution and access and training [animal health professionals] and households on appropriate vaccine storage and handling” are key factors to increasing low vaccine uptake in this region (Williams *et al.*, 2022).

Future research priorities

Based on the available literature, expert opinion, and previously published reviews, we suggest that the following areas of research into SPPV and GTPV should be considered high priority:

Biology of the pathogen

- Continued characterisation of viral gene products
- Ongoing translation of general poxvirus knowledge (e.g., of VACV) into SPPV and GTPV, including assessment of homologous proteins

Diagnosis

- Novel DIVA assays must be tested fully and thoroughly to establish their range of applicability and accuracy under different situations including different sample types and virus/vaccine combinations, as conducted by Byadovskaya and colleagues in 2020 for the then-available commercial and published tests (Byadovskaya *et al.*, 2020)
- Validation of new serological tests on large sample-sets; protocols that are easy to use in low-resource settings without specialised biosafety facilities should be favoured
- Development of integrated control program where vaccination/diagnostics/DIVA/molecular monitoring of emerging strains work together to eradicate/manage disease

Pathogenesis

- Studying the causes of low vs. high mortality outbreaks (e.g., different viral strains, different small ruminant breeds, different environmental and/or farm management conditions, etc.)
- Understanding the viral mechanisms and host-pathogen interactions underlying the higher mortality of GTP in goats compared to SPP in sheep

Immunology

- Data on microbiota have dual implications: more research is required into the potential link between antibiotic overuse and/or misuse and lower responses to veterinary vaccines. Probiotic supplementation/improved diet could simultaneously render animals more well and more able to be protected by vaccines
- Despite strong evidence that cattle breeds are differentially susceptible to LSD, we could not find any studies aiming to understand the genetic basis of the difference. Such information could prove valuable in planning selective breeding programs for increased disease resistance
- More focus is needed on the immunology of subclinical infections to inform vaccine responses

Epidemiology

- Mapping of SPPV transmission networks across the borders between Turkey and neighbouring European countries
- Establishing and expanding disease surveillance networks in resource-limited regions like northern Africa and Southeast Asia
- Expansion of participatory epidemiology among rural small ruminant farming communities to ensure effective implementation of disease control strategies (e.g., vaccination campaigns)

Control

- Need increased focus on standardised testing and reporting approaches; inclusion of sufficient data in published manuscripts to accurately interpret the results (e.g., the virus strains used, the vaccines compared, etc.); avoidance of highly artificial challenge models in non-target species; and avoidance of low-level immunological readouts that miss the opportunity to advance our knowledge of the immune response to the virus itself, to the vaccines being tested, and to the interaction between the two
- Identification of protective antigens to facilitate exploration of vectored and mRNA vaccine approaches
- Continuing development of vaccines that with particular emphasis on affordability and availability; thermal stability; ease of application; and high efficacy without severe side effects
- Exploring combinations of inactivated and live-attenuated vaccines to potentially reduce side effects and retain efficacy
- Long-range studies
- Inter-breed differences
- Incorporation of recent events (e.g., SPP outbreaks in Spain and Kosovo) into risk assessment models for introduction of SPP and GTP to naïve small ruminant populations

Review conclusions

The studies cited above illustrate the immense amount of research conducted into CaPV over the past decade, as the geographical range of these viruses continues to grow. Significant strides have been made in our understanding of the basic biology of these viruses, the determinants of their virulence, and their interactions with host cells and immune pathways. These in turn have facilitated more efficient diagnostics and the production of vaccine candidates that improve efficacy and/or reduce safety concerns. Continuing advances in nucleic acid sequencing and computational modelling have also provided new avenues for tracking viral evolution and predicting risk factors for outbreaks in endemic regions and for introduction to naïve ones.

Despite this, our knowledge of CaPV epidemiology remains severely limited in rural areas including much of Africa, Southeast Asia, and remote regions of China and India. Farmer engagement, training of sufficient numbers of veterinarians and integrated diagnostic and reporting strategies are much needed. The large ruminant populations and importance of livestock farming in these areas ensures that CaPV will continue to spread and transmit unless these limitations are resolved. The deployment of effective surveillance in remote areas is not a simple task, and neither is the degree of international and regional cooperation required to ensure adequate biosecurity and disease control at the international borders across which ruminant herds frequently move unmonitored. While prevalence reports from rural and/or remote areas are becoming more common, there is an urgent need to integrate these small-scale studies and produce a unified picture of CaPV transmission patterns and risk factors.

Several intertwined research questions and policy problems stand in the way of effective CaPV control. Many of these questions fall under the general purview of participatory epidemiology: for instance, what price is considered affordable for a CaPV vaccine? What drives farmer engagement/disengagement with vaccination programmes? What are the impacts of educational outreach and training programmes for farmers and local veterinarians? Notably, the answers to many/all of these questions will be different in different geographical regions – it will be important not to overgeneralise results from one population to another.

The development of technologies for monitoring and controlling CaPV has also been uneven. Numerous DIVA-compatible CaPV diagnostics are already available, but vaccines are less accessible. Concerted forward movement of the vaccine field is often confounded by the absence of a standardised approach to testing or agreed-upon reporting methods. While there are examples of excellence within the literature, a high proportion of papers are published with: insufficient experimental detail to accurately interpret the results; use of highly artificial challenge models in non-target species; and with low level immunological readouts that miss the opportunity to advance our knowledge of the immune response to the virus itself, to the vaccines being tested, and to the interaction between the two. The field also suffers from a high barrier between development and deployment, with many examples of ostensibly promising vaccine candidates that do

not proceed further into testing. Progress from development to validation and field deployment will require vaccine study funding approaches that prioritise well-conducted “next steps” studies to advance the development of novel vaccines that have shown promise in preliminary trials, rather than more studies trialling variations.

Though the problem is particularly pronounced for vaccine studies, all aspects of CaPV research suffer from a lack of available funding relative to many other significant livestock pathogens. While dedicated international research alliances have been created to organise and spearhead research into FMDV and ASFV, for instance, no such institutions currently exist for CaPV. At the government level, lack of knowledge on these viruses and unwillingness to fund the expensive research needed to study immunology and vaccine efficacy in live cattle hamper the development of control capabilities (S. Babiuk, personal communication).

CaPV pose a serious threat to the economic security of animal production systems across much of the world. From a One Health perspective, it is also important to note that although these are viral diseases, there is a clear intersection with the current overuse of antibiotics in agriculture. The skin lesions caused by CaPV are susceptible to secondary bacterial infection and, in the absence of effective treatment for the underlying condition, several antibiotics are often used to prevent or treat these complications.

Altogether, our understanding of CaPV biology, epidemiology, and control have grown substantially over the past decade. The studies discussed in the above report encourage optimism in the progress that has been made while emphasising the need for increased standardisation and coordination between laboratories and nations in CaPV control. The authors of this report hope that it will serve as a valuable resource for researchers, policymakers and other private and public stakeholders pursuing these collaborative goals.

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Appendices

Abbreviations

AHAW	Animal Health and Welfare panel
ASFV	African swine fever virus
BEI	Binary ethyleneimine
BHK-21	Baby hamster kidney-21
BoLA	Bovine leukocyte antigen
bp	Base pairs
BTV	Bluetongue virus
CaPV	Capripoxvirus
cGAS	cyclic GMP-AMP synthase
CNN	Convolutional neural network
CRISPR	Clustered regularly interspaced short palindromic repeat
DIVA	Differentiation of infected from vaccinated animals
DNA	Deoxyribonucleic acid
dsDNA	double-stranded DNA
EEV	Extracellular enveloped virus/virion
EFSA	European Food Safety Authority
ELISA	Enzyme-linked immunosorbent assay
FAO	Food and Agriculture Organisation
FMD	Foot-and-mouth disease
GFP	Green fluorescent protein
GM-CSF	Granulocyte-macrophage colony-stimulating factor
GPCR	G protein-coupled receptor
GTP	Goatpox
GTPV	Goatpox virus
HEK	Human embryonic kidney
HRM	High-resolution melting
IFIT	Interferon-induced protein with tetratricopeptide repeats
IFN	Interferon

IL	Interleukin
IRF	Interferon regulatory factor
ISG	Interferon-stimulated gene
ITR	Inverted terminal repeat
KSGP	Kenyan sheep and goat pox
LAMP	Loop-mediated isothermal amplification
LAV	Live attenuated vaccine
LMIC	Low- and middle-income country
LSD	Lumpy skin disease
LSDV	Lumpy skin disease virus
MaxEnt	Maximum entropy
MDBK	Madin-Darby bovine kidney
miRNA	microRNA
mRNA	Messenger RNA
OBP	Onderstepoort Biological Products
ORF	Open reading frame
PBMC	Peripheral blood mononuclear cells
PCR	Polymerase chain reaction
PPR	Peste des petits ruminants
PPRV	PPR virus
qPCR	quantitative real-time PCR
RNA	Ribonucleic acid
piRNA	piwi-interacting RNA
PPRV	Peste des petits ruminants virus
RPA	Recombinase polymerase amplification
SPP	Sheeppox
SPPV	Sheeppox virus
STING	Stimulator of interferon genes
TBK1	TANK-binding kinase 1
TNF	Tumour necrosis factor
VACV	Vaccinia virus
VI	Virus isolation
VNT	Virus neutralisation test
WOAH	World Organisation for Animal Health

Details of searches

The literature search terms provided below were used to interrogate the CAB Abstracts database (www.cabdirect.org) on 3rd March 2026. The searches were supplemented using the PubMed database (https://pubmed.ncbi.nlm.nih.gov/) (which has a shorter lag time between publication and updating) weekly, from 3rd March 2026 until the 18th June 2026, to capture any new literature published during the report-writing period.

CAB Abstracts search terms

(Indexingterm:(“lumpy skin disease” OR “goat pox” OR “sheep pox” OR “Sheeppox virus” OR “Goatpox virus” OR “lumpy skin disease virus” OR Capripoxvirus) OR et:(“lumpy skin disease” OR “goat pox” OR “sheep pox” OR “Sheeppox virus” OR “Goatpox virus” OR “lumpy skin disease virus” OR Capripoxvirus)) AND yr:(2015 OR 2016 OR 2017 OR 2018 OR 2019 OR 202*)

PubMed search terms

Search: "lumpy skin disease"[Title] OR "goat pox"[Title] OR "sheep pox"[Title] OR "Sheeppox virus"[Title] OR "Goatpox virus"[Title] OR "lumpy skin disease virus"[Title] OR "Capripoxvirus"[Title]

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Conflict of Interest Statement

The authors declare no conflict of interest.