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Review

Transmission of lumpy skin disease virus: A short review

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ABSTRACT

Lumpy skin disease (LSD) is a viral transboundary disease endemic throughout Africa and of high economic importance that affects cattle and domestic water buffaloes. Since 2012, the disease has spread rapidly and widely throughout the Middle Eastern and Balkan regions, southern Caucasus and parts of the Russian Federation. Before vaccination campaigns took their full effect, the disease continued spreading from region to region, mainly showing seasonal patterns despite implementing control and eradication measures. The disease is capable of appearing several hundred kilometers away from initial (focal) outbreak sites within a short time period. These incursions have triggered a long-awaited renewed scientific interest in LSD resulting in the initiation of novel research into broad aspects of the disease, including epidemiology, modes of transmission and associated risk factors. Long-distance dispersal of LSDV seems to occur via the movement of infected animals, but distinct seasonal patterns indicate that arthropod-borne transmission is most likely responsible for the swift and aggressive short-distance spread of the disease. Elucidating the mechanisms of transmission of LSDV will enable the development of more targeted and effective actions for containment and eradication of the virus. The mode of vector-borne transmission of the disease is most likely mechanical, but there is no clear-cut evidence to confirm or disprove this assumption. To date, the most likely vectors for LSDV transmission are blood-sucking arthropods such as stable flies (*Stomoxys calcitrans*), mosquitoes (*Aedes aegypti*), and hard ticks (*Rhipicephalus* and *Amblyomma* species). New evidence suggests that the ubiquitous, synanthropic house fly, *Musca domestica*, may also play a role in LSDV transmission, but this has not yet been tested in a clinical setting. The aim of this review is to compile and discuss the earlier as well as the most recent research data on the transmission of LSDV.

1. Introduction

The recent spread of lumpy skin disease (LSD) into climatically new and previously disease-free regions underlines the importance of developing an in-depth understanding of the transmission mechanisms of the virus, contributing towards improved control and eradication of the disease.

Effective containment of the recent spread of LSD virus (LSDV) within the Balkans showed that vaccination using live attenuated vaccines is safe, and it provides, by far, the best tool for LSD control. However, the use of live vaccines always has the risk, in the evolutionary perspective, that the vaccine virus may regain virulence by recombining with virulent field strains upon coinfection (Sprygin et al., 2018c), or the vaccine product itself may be contaminated during the production process by extraneous viruses that are harmful to cattle, such as pestiviruses. Thus, other supporting and safer methods to prevent the spread of the disease should be sought, warranting further studies such as ones to enable a thorough understanding of the different transmission routes.

Poxviruses are known for their ability to use various direct or indirect means to infect their hosts, such as through direct contact, via exposure to aerosols produced by infected hosts, through semen or via intrauterine infection. Transmission can also occur indirectly via a contaminated environment, fomites, or vectors. Transmission pathways vary between different genera within the *Poxviridae* family and also within a genus, as exemplified by capripoxviruses (Buller et al., 2005).

Since the earliest outbreaks of LSD in southern Africa and the African Horn sub-regions, long-distance dispersal of the virus has been associated with movement of clinically and sub-clinically ill cattle via transport along roads, railways, and on foot due to animals being herded long distances to markets or seasonal grazing lands. The seasonality of outbreaks has increased suspicions that local virus dissemination is associated with the activity and abundance of vectors (Weiss, 1968).

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Turkey has historically served as a gateway for trade and migration, which consequently enables the inadvertent introduction of exotic diseases from Asia to Europe. The precise source from which the LSD infection was introduced to Turkey in 2013 has not been identified with certainty. It has been speculated that cattle trafficking, coupled with the influx of more than two million refugees from war-torn neighboring countries, resulted in the introduction of an uninvited "guest" that has widely affected the local naïve cattle population (Sevik and Dogan, 2017; Albayrak et al., 2018). Turkish scientists suggested that the trade in unvaccinated animals already incubating LSD virus could explain the long geographical jumps the virus has made within the country, such as the first outbreaks reported in Catova village in Kahramanmaras district in Turkey located approximately 200 km from the Syrian border (Saraç et al., 2017; Sevik and Dogan, 2017). Slow disease reporting by farmers facilitated the free spread of the virus by delaying the implementation of control measures (Ince et al., 2016). Transhumant nomadic and seminomadic pastoralism are hereditary practices, particularly in southeastern Turkey and Caucasus, that involve traditional routes to summer and winter pastures. Long-distance transhumant movement of cattle herds along migratory routes is considered to be an especially high risk factor for disease spread (Ince et al., 2016). Moreover, in a recent epidemiological study of LSD outbreaks in Russia, three cases were identified that occurred more than 800 km away from the outbreak epicenter, suggesting vehicle-assisted transport of infected animals (Sprygin et al., 2018a).

After the initial introduction of infected animal(s) into a new region, the virus needs to be effectively disseminated to the susceptible cattle in the surrounding farms or environments for an outbreak to initiate and manifest. The data collected during the Balkan LSD outbreaks indicate that short-distance spread (approximately 7.3 km per week) was associated with cattle movements and presence of vectors (Mercier et al., 2018).

Spontaneous movements of flying arthropods seem to be a significant factor in the spread of the disease over short distances. Biting or blood-sucking arthropods, such as mosquitoes and dipterans, are likely to vector viruses at distances that correlate with their flight capabilities (Burdin and Prydie, 1959; Macowan, 1959). For example, less than 5% of captured-tagged stable flies (*Stomoxys calcitrans*) were recaptured more than 5 km from where they were released (Taylor et al., 2010). In addition, the ratio of the abundance of biting insects to the abundance of hosts is positively correlated with transmission probability (Gubbins et al., 2008).

Most blood-sucking insects can fly up to a maximum of 100 m if unassisted by air movements (Greenberg et al., 2012). Thus, the direction and strength of winds may contribute to the spread of the virus by flying insects over longer distances (Rouby and Aboulsoud, 2016; Chihota et al., 2001, 2003). An analysis of LSD outbreaks in Israel showed that the onset of clinical symptoms likely followed a windborne dispersal of virus-carrying vectors (Klausner et al., 2017). However, because vector transmission is considered to be of a mechanical nature and the numbers of infective viruses on insects' mouthparts is likely to be low, in the absence of other supporting factors, air currents would need to transfer hundreds of contaminated vectors onto a single susceptible animal to induce full clinical disease. Furthermore, the duration for which a virus can survive in an insect's mouthparts is unknown. Therefore, wind-aided virus transmission by arthropod vectors is unlikely to play a significant role in long-distance disease spread.

The aim of this review is to summarize the current knowledge of LSDV transmission obtained from the field and experimental studies and identify areas in which further research is still required. A synopsis of potential transmission modes follows.

2. Direct and indirect modes of transmission, non-vectored

Generally, direct contact has been shown to be an ineffective route for the transmission of LSDV, but actual experimental evidence is scarce. Early experimental work and field observations in South Africa led to the conclusion that LSDV transmission by direct contact probably occurs, although at low rates and efficiency (Diesel, 1949; Weiss, 1968). This is supported by observations of LSD outbreaks occurring outside the window of optimal insect activity temperatures (World Animal Health Information Database (WAHID, 2018). By contrast, declines in LSDV infection rates during dry or cold seasons, which are associated with low numbers or the absence of insects, are reported (Nawathe et al., 1982; Kondela et al., 1984) and failed attempts to contain LSD outbreaks by controlling cattle movement, provides circumstantial evidence that the virus is disseminated by vectors (Diesel, 1949; Nawathe et al., 1982), However, sharing of water sources and the introduction of new animals into a herd also appears to increase the risk of LSD outbreaks (Macowan, 1959; Ali and Obeid, 1977). Although these early observations are accurate, they are mainly based on the observation of clinical signs. Virus isolation and other diagnostic methods available at that time were of relatively low sensitivity compared to modern molecular analytical tools available today.

Carn and Kitching (1995) investigated the direct-contact transmission route of LSDV by performing seven separate experiments, where in each experiment one uninfected cow was housed in close contact with two infected animals for a month. None of these in-contact animals developed clinical signs or produced detectable levels of serum neutralizing antibodies. When these animals were then challenged (infected) with virulent LSDV, six of the seven were completely susceptible to infection, showing no delayed type hypersensitivity. However, the number of in-contact animals in this study was too low to draw definitive conclusions. In addition, of the first-stage infected animals, severe generalized infection in both animals was only observed in two of the seven experiments, and in one experiment only in one of the infected animals, and it is unknown whether they had any lesions in their oral or nasal mucosal membranes or were excreting infective virus in their saliva and/or nasal discharge.

During an LSD outbreak on a dairy farm in Israel in 2006, researchers used mathematical modeling to investigate the possible different modes of transmission (Magori-Cohen et al., 2012). They concluded that direct animal-to-animal contact did not play a significant role in transmission, because no positive correlation was found between cattle density and infection rates, whereas the observed pattern of spread was explainable by indirect transmission, probably by blood-sucking insects. However, all animals showing severe clinical disease were removed from the herd without delay, which may have artificially reduced any effects of animal-to-animal contact.

Because only approximately one third of experimental animals exhibit severe clinical disease after inoculation with virulent LSDV, transmission studies are complicated to design and expensive to perform in an experimental setting. For example, to achieve severe infection with generalized clinical signs in just three animals, approximately nine need to be infected with a highly virulent LSDV isolate using both the intradermal and intravenous routes. To simulate field outbreaks, experimental cattle that are intended to serve as infection sources for naïve animals need to exhibit severe infection with multiple lumps in their skin and ulcerative lesions in the mucous membranes of their mouths and nasal cavities. Only then can these animals be expected to excrete sufficient quantities of infectious viruses in their nasal discharge and saliva.

Interestingly, direct contact with virus-containing droplets and aerosols is an important route of virus dissemination for the other members of the *Capripoxvirus* genus, sheeppox (SPP) and goatpox (GTP) viruses (Carn and Kitching, 1995; Kitching and Taylor, 1985). Indirect LSDV transmission might occur when cattle are sharing feed or water troughs contaminated by saliva or nasal discharge from infected animals (Weiss, 1968; Ali et al., 2012). Babiuk and co-workers (2008) demonstrated only low levels of virus in oral and nasal secretions 12–18 days post-infection. It should be noted that these experimental animals exhibited only a mild form of LSD, with only approximately 25% of their skin surface being covered with nodules. However, high virus loads, comparable to those in skin lesions, were found in the mucous membranes of the mouth and nose (Babiuk et al., 2008). In another study, Prozesky and Barnard (1982) reported several lesions in the mouth, nostrils, pharynx, larynx, and trachea characterized by erosion and ulceration in severely infected animals. These erosions and ulcerations are likely to serve as virus sources into the saliva and nasal discharge, and infectious viruses are likely to persist in aerosols and droplets originating from these animals.

However, experience in the field has shown that the saliva and nasal swabs are good sampling materials, equal to those obtained from the skin (Dietze et al., 2018). Thus, while low virus titers within nasal or other discharges are indeed likely to lower the risk of contact transmission, there is a need to re-investigate the direct mode of transmission as it pertains to spread of LSDV.

Intrauterine transmission of LSDV has been documented recently (Rouby and Aboulsoud, 2016) and transmission from mother to calf via contaminated milk or skin lesions on the mother's udder and teats are also likely to occur (Tuppurainen et al., 2017) but there is a need to experimentally confirm this assumption.

LSDV has been isolated from the semen of experimentally-infected bulls 22 days post-infection (dpi) (Weiss, 1968). Results from a more recent study demonstrated the persistence of live virus in bovine semen for up to 42 dpi, and viral DNA was detected up to 159 dpi (Irons et al., 2005). Transmission via contaminated bovine semen has been experimentally demonstrated (Annandale et al., 2013), and consequently, artificial insemination or natural mating should be considered as risk factors for transmission during an outbreak. Vaccination using a homologous vaccine seemed to eliminate the virus from semen, and the vaccine virus was also not detected in semen samples (Osuagwuh et al., 2007).

Carn and Kitching (1995) performed intradermal inoculation trials of LSDV in cattle and found that generalized disease occurred in less than 20% of cases, whereas the remaining animals exhibited only localized disease. In contrast, the intravenous route of LSDV inoculation produced generalized disease in 70% of animals. In a trial conducted on only two experimental animals, infection was not achieved through the conjunctival sac (Carn and Kitching, 1995). These findings suggest that a successful infection cycle requires inoculation into the bloodstream, which is a typical route in insects feeding from the lumen of a blood vessel.

Transmission of LSDV by contaminated needles used during vaccination campaigns is often suggested as a potential mechanism for the spread of infection within a herd (Tuppurainen et al., 2017). Experimental infection of cattle requires high viral loads to be administered via both intravenous and subcutaneous routes. The actual volume of virus inoculated by a single needle stick occurrence would most likely be too low to result in clinical disease, even in the event of successful virus transmission. Vaccination programs are often started late, when the disease is already widely circulating in a region and there is more than one infected animal in the herd. It is actually very difficult to evaluate with certainty the role of the iatrogenic mode of transmission in a field setting. In addition, it is highly likely that inoculating a vaccine virus into an already infected animal is likely to make the natural infection even worse.

Thus, these results suggest that further transmission studies are required to completely understand the role of direct contact, including the possibility of detecting subclinical infections. For such studies to be relevant, they will likely require use of a highly virulent LSDV field strain, sensitive molecular methods for detecting viral antigens, and long duration of the experiment, and sufficient numbers of experimental animals.

3. Insect transmission

Mechanical transmission by arthropod vectors has been reported for several poxviruses, such as fowlpox (Brody, 1936), myxoma (Fenner et al., 1952), and swinepox viruses (Tripathy et al., 1981). Rabbit (Shope) fibroma virus is readily transmitted mechanically by mosquitoes, fleas and other biting arthropods (Kilham and Dalmat, 1955). In all these cases, the viruses were associated with the arthropod's mouthparts and head region, but not its body.

Vector competence depends on, but is not limited to, the probability of feeding activity and frequency of biting habits, vector abundance, and host availability (Kahana-Sutin et al., 2017).

To date, only mechanical transmission is implicated for LSDV. However, some field observations have suggested that the possibility of a biological mode of transmission of the virus by *Culicoides* midges exists and should thus be investigated. During the 2014–2015 outbreaks in Turkey, non-engorged *Culicoides punctatus* (Latreille; Diptera: *Ceratopogonidae*) females were collected from outbreak farms that tested positive for LSDV DNA. However, pools of midges also tested negative for ruminant beta-actin mRNA, providing evidence that they had not recently been feeding on bovines at the time of viral DNA acquisition (Sevik and Dogan, 2017).

The mechanical mode of transmission is not as closely associated with one or a limited number of vector species as is biological transmission (Gray and Banerjee, 1999a). In principle, any local vector species that prefers cattle and frequently changes hosts could carry infectious virus in its mouthparts, emphasizing the importance of an in-depth understanding of the biology, feeding preferences, and habits of local arthropod species.

It is typical for LSD that experimental infection of cattle requires inoculation of virulent virus at high titers via both intravenous and intradermal routes, although, only 70% of the animals typically develop a severe clinical disease (Carn and Kitching, 1995; Tuppurainen et al., 2005). Therefore, successful mechanical transmission probably requires tens or hundreds of bites from blood-feeding vectors to pass on the virus contained in their contaminated mouthparts. However, there have been no reported studies to date on the role of arthropod saliva and its effect on the host immune response against LSDV at the vector's feeding site, which may in fact reduce the number of virus required for transmission.

A general prerequisite for an arthropod to act as a mechanical vector is its presence in high numbers at an outbreak site (Kahana-Sutin et al., 2017). In cases of interrupted feeding prior to engorgement, the feeding arthropod needs to find another host, thus, providing an opportunity to pass on the virus. It is still unknown whether mechanical transmission is simply achieved by mouthpart contamination or whether more complex interactions are required. In severely infected animals, skin lesions are known to contain high titers of virus (Babiuk et al., 2008), providing a plentiful source of contamination for biting and blood-feeding arthropods. For insects, such as mosquitoes, which feed directly from blood vessels, the level of viremia in LSD infected host is usually low, and viraemic stage lasts for less than 12 days (Tuppurainen et al., 2005). On the other hand, these insects inoculate the virus directly into the blood stream which may in turn enhance their infectivity. Very high numbers of mosquitoes were present in the wetlands of the Thrace region where the first European LSD outbreaks were detected in 2015 (Tasioudi et al., 2016), however outbreaks do also occur outside the vector prevalence period (May to August), arguing for another yet overlooked transmission means (World Animal Health Information Database (WAHID, 2018).

The efficacy of mechanical vectors' viral transmission also depends on the length of time that the infectious virus can survive on the surface of the mouthparts, salivary glands, or even in the foregut. Furthermore, it is possible that for LSDV, some yet unknown vector-borne factors, such as saliva, may affect the efficacy of the proposed mechanical transmission.

Open skin lesions and ulcers offer an attractive source of nutrients for flies (Kugler, 1969). Infectious LSD viruses are known to survive in skin lesions for at least 39 days post-infection (Tuppurainen et al., 2005). In addition, the live virus is also present in the healthy-looking skin regions of infected cattle (Babiuk et al., 2008). Because vectors may feed on the skin lesions of naturally-infected cattle or on the local lesion formed at vaccine inoculation sites, the vector's mouthparts could become contaminated with a virulent field virus or attenuated vaccine virus.

The common stable fly (*S. calcitrans*), with a global distribution, is the most widely suspected vector species for LSDV spread (Weiss, 1968; Kitching and Mellor, 1986; Kahana-Sutin et al., 2017; Yeruham et al., 1995; Davies, 1991). Transmission of the virus by *Aedes aegypti* mosquitoes (Chihota et al., 2001) and some African hard tick species has also been reported (Tuppurainen et al., 2010). Recently, novel evidence on the potential role of non-biting flies has been presented (Sprygin et al., 2018b).

Stable flies are aggressive and persistent feeders and, since their bites are painful, feeding is often interrupted by the host, requiring flies to continue on another host. Thus, stable flies usually require three to five feeding attempts to achieve satiety (Schofield and Torr, 2002).

Live virus has been isolated and identified using PCR from stable flies either directly and 24 h post-feeding on infected cattle (Weiss, 1968; Chihota et al., 2003), and still the actual transmission of LSDV by this vector remains to be conclusively demonstrated in an experimental setting. Kitching and Mellor (1986) demonstrated the mechanical transmission of SPP and GTP viruses by *S. calcitrans*, so it would be surprising if this does not occur with LSDV as well.

During the 1989 LSD outbreak in Peduyim, Israel, it was suggested that the infection originated from a concurrent outbreak in Ismailiya, located over 85 kms away or in El Arish in northern Sinai, Egypt. The virus was suspected to be introduced by contaminated stable flies, carried by prevailing winds or inside cattle transport vehicles (Yeruham et al., 1995).

In another Israeli study, a high relative abundance of stable flies in November-January and March-April 2012–2013, correlated with LSD outbreaks on dairy farms (Kahana-Sutin et al., 2017). Between October and November, when the numbers of *S. calcitrans* dropped, LSD was detected in adjacent beef herds, suggesting the possibility that other vectors, such as a horn fly, *Haematobia irritans*, could have played a role in transmitting the virus. This suggestion was based on the concomitant observation of abundant fly populations in areas where beef cattle were being kept (Kahana-Sutin et al., 2017). Thus, the role of horn flies in the transmission of LSDV should also be examined in an experimental setting.

The housefly, *Musca domestica*, seems to be capable of vectoring viral and bacterial pathogens of livestock (Pitkin et al., 2009; Barin et al., 2010). When the proboscises of non-biting flies becomes contaminated after feeding on well-developed skin lesions in myxomatosis-affected rabbits, these insects are able to transfer the disease (Fenner et al., 1952). There have only been a few studies on the potential role of non-blood-feeding insects as vectors of LSDV. Non-biting flies could also possibly act as inadvertent vectors by feeding on the carcasses of cattle having recently died of LSD or were culled due to LSD, thereby taking up the virus from open skin lesions or body fluids containing high virus titers (Sprygin et al., 2018b). A non-biting fly, *Biomya fasciata*, has been implicated as a possible vector for LSDV, since the virus was isolated from flies collected from infected cattle in the field, as well as three days after being artificially fed virus-spiked blood (Weiss, 1968). During an LSD outbreak in Russia in 2017, ubiquitous, synanthropic houseflies, *M. domestica* L. (Diptera: Muscidae), tested positive for the presence of vaccine-like LSDV genomic DNA (Sprygin et al., 2018a).

As early as 1957, mosquitoes were suspected to play a role in LSD transmission when Burdin and Prydie (1959) reported that LSD outbreaks in Kenya were associated with a high incidence of *Aedes natronius* and *Culex mirificus* mosquitoes.

Culex spp. mosquitoes have been shown to feed multiple times on different hosts, offering the opportunity for them to become infected and pass the pathogen onto a naïve host. Some scientists have reported that mosquitoes are unlikely to return to the original host as a defensive behavior (Anderson and Brust, 1997), thereby increasing the probability of transmission.

Culex quinquefasciatus Say (Diptera: Culicidae) and *Anopheles stephensi* Liston (Diptera: Culicidae) have also tested positive for LSDV using PCR, a few days after feeding on infected animals, although they failed to transmit the virus experimentally (Chihota et al., 2003).

Mosquitoes and sandflies feed directly from small blood vessels and can, therefore, intravenously inject LSDV (Carn and Kitching, 1995). After feeding on LSDV-rich skin lesions, *A. aegypti* mosquitoes were shown to transfer the virus to susceptible cattle over a period of two to six days (Chihota et al., 2001). In cases where an insect performs multiple blood meals from a few hosts, it is highly likely that other mosquito species present, such as occurs in the Middle East and currently affected areas in Europe, Russia and Caucasus, may serve as mechanical vectors for LSD. For example, myxoma virus has been shown to be transmitted by several mosquito species for extended periods, and multiple inoculations from a single insect have been documented (Gray and Banerjee, 1999a). Interestingly, the efficiency of transmission differs among mosquito species regardless of the titer of the virus in the blood that mosquitoes imbibed (Fenner and Ratcliffe, 1965; Gray and Banerjee, 1999b).

Friedberg (1985) suggested that horse (*Tabanidae*), horn (*Haematobia irritans* [L.]), and louse (*Hippoboscidae*) flies may act as potential vectors for several diseases in Israel, and LSD viral DNA has been reported in *Tabanus spodopterus* females (Alexandrov, 2016)

In related studies, attempts to transmit SPP virus by biting lice (*Mallophaga* spp.), sucking lice (*Damalinia* spp.), sheep head flies (*Hydrotaea irritans*), and midges (*Culicoides nubeculosus*) were unsuccessful, although the virus has been isolated from sheep head flies that had previously fed on infected sheep (Kitching and Mellor, 1986).

Systematic surveillance of the abundance and activity levels of suspected vector species could provide essential data for risk assessment. Several research projects investigating potential vectors for LSDV are currently on-going, and within the next few years these should lead to a substantial increase in our understanding of the vector transmission of LSDV in the northern hemisphere.

4. Tick transmission

The survival of a virus in tick vectors depends on the susceptibility of tick cells to infection with the virus and the ability of the virus to withstand histolysis in tick tissues (Labuda and Nuttall, 2004). As with insect vectors, transmission of the virus by ticks may be mechanical, in cases where the singe tick feeds several times and change host between the feeds. Fowlpox virus provides an example of mechanical transmission of a poxvirus by ticks (Shirinov et al., 1969).

The biology of the tick is complex and varies between different tick species. In general, adult three-host female ticks, nymphs and larvae feed only once on a host and then detach and drop off. The next feeding occurs at the next life-cycle stage and on a different host. As an exception, adult males of several common hard (ixodid) tick species take multiple small blood-meals while looking for females suitable for mating. They do so on one individual host, or if cattle come into close skin-to-skin contact they can also swiftly and easily change hosts (Tuppurainen et al., 2010). In favorable circumstances, females may also feed on more than one host, for example if the host dies or if vigorous grooming by the host interrupts the feeding at an early stage (Wang et al., 1998).

Mechanical transmission of LSDV from infected to naïve hosts has been experimentally demonstrated in *Rhipicephalus appendiculatus* (Tuppurainen et al., 2013a) and *Amblyomma hebraeum* (Lubinga et al., 2013b) male ticks.

The presence of LSDV has been demonstrated in tick saliva after feeding on infected cattle (Lubinga et al., 2013b), and transstadial transmission of the virus has also been reported (Lubinga et al., 2014b).

Tick molting seems to reduce virus titers. The LSD viral antigen has also been demonstrated using immunohistochemical methods in tick salivary glands, hemocytes, synganglia, ovaries, testes, fat bodies, and midgut. (Lubinga et al., 2014a).

Rhipicephalus decoloratus is a one-host tick and all three of its lifecycle stages occur on the same host. After feeding on infected cattle, the females were able to transmit LSDV via their eggs to the next generation of larvae, which in turn were able to infect naïve cattle (Tuppurainen et al., 2013b). The exact mechanism of transmission, however, needs further investigation as LSDV is very stable and this may actually constitute mechanical transmission (Tuppurainen et al., 2015). Similarly, *Hyalomma truncatum* ticks sexually transmit Crimean-Congo hemorrhagic fever virus (Gonzalez et al., 1992). During interrupted feeding on the skin of an infected animal, the male's mouthparts become contaminated with the virus. Since the male places its semen sack into the female's genital openings with its mouthparts, it also contaminates the female during copulation (Varma, 1993). LSDV has also been shown to be transmitted transovarially in ticks following exposure to cold temperatures that imitate natural overwintering conditions (Lubinga et al., 2013a, b; Lubinga et al., 2014c).

More recent studies have provided further evidence of a similar type of transmission in *R. annulatus* ticks. Engorged *R. annulatus* females were collected from LSDV-infected cattle in the field, and females were allowed to oviposit. Live virus was then isolated from subsequent larvae on chorioallantoic membranes of embryonated hen eggs (Rouby et al., 2017).

Environmental factors in central and southern Africa are favorable for the maintenance and proliferation of ticks, and ticks remain active for longer than, for example, in the Middle East (Parola et al., 2008). In addition, communal grazing practices that allow cattle to share the same pastures with other herds and/or wild ruminants are likely to support the transmission of LSDV by ticks. However, the tick species *R. appendiculatus* and *A. hebraeum,* which have been used in studies to date, are currently restricted to Africa (Tuppurainen et al., 2013a; Lubinga et al., 2013b).

During the recent outbreaks of LSD in the northern hemisphere in the Republic of Dagestan and Kabardino-Balkaria in Russia, the presence of LSDV DNA was detected in at least 13 species of ixodid ticks, belonging to six genera: *Hyalomma* Koch, 1844; *Dermacentor* Koch, 1844; *Ixodes* Latreille, 1795; *Boophilus* Curtice, 1891; *Rhipicephalus* Koch, 1844; and *Haemaphysalis* Koch, 1844. The LSDV genome was frequently detected in *I. ricinus* (16.3% of ticks tested), *B. annulatus* (14.3%), *D. marginatus* (13.8%), *Hyalomma marginatum* (11.6%) and *Haemaphysalis scupense* (8.1%). This led to the conclusion that ixodid ticks may have played a role as vectors or reservoirs for LSDV during the 2015 outbreaks, but more detailed studies would be required to confirm these tentative findings (Gazimagomedov et al., 2017). The duration of the tick life cycle is unlikely to fully explain the speed at which epidemics unfolded during the recent outbreaks in Russia (Sprygin et al., 2018b). LSDV DNA was detected in *Hyalomma marginatum* females *and Rhipicephalus bursa* males and females during surveillance in Bulgaria (Alexandrov, 2016).

The first outbreaks of LSD in Europe have led to an increase in research on potential arthropod vectors of LSDV. Further studies in an experimental environment are required to fully understand the vector capacity and potential role of ticks as reservoirs of LSDV in northern climes.

5. Conclusion

Only mass vaccinations were able to stop the spread of LSD in the Balkans from 2015–2017. An in-depth understanding of the various transmission mechanisms of LSDV and the role of local vector species could assist in limiting the spread of the disease at a very early stage, and thus, prevent large-scale transboundary dissemination. It would also provide much needed data to help farmers implement well-targeted biosecurity measures to protect their cattle in case of an outbreak.

The scientific literature suggests that arthropod transmission of LSDV is the most likely strategy by which the virus spreads, a conjecture that is supported by the seasonality of outbreaks, which are distinctly associated with warm and rainy conditions. Intravenous inoculation of LSDV produces pronounced clinical symptoms in experimentally infected hosts when compared with intradermal inoculations (Carn and Kitching, 1995), and so vectors such as mosquitoes that feed directly through blood vessels are likely vector candidates (Lavoipierre, 1965). In most cases the long-distance spread of LSDV is associated with animal movements. Novel vectors remain to be discovered and the LSDV vectoring potential of abundant dipteran pests associated with cattle, such as flies, should be evaluated.

Despite evidence for vector-borne transmission, outbreaks may also occur in the apparent absence of vectors, highlighting that vector-borne transmission is not the only mode of LSDV transmission. Occasional reports of the direct transmission of LSDV suggest that no season should be considered absolutely safe with respect to LSD.

It may be too optimistic to assume that the identification of the main vector species would be sufficient to forego the use of vaccines, but it would certainly help in decreasing disease prevalence. A better understanding of the feeding habits and preferences of local blood-feeding and biting vectors, the survival of the infectious virus in those vectors, and capacity of local arthropod species to operate as mechanical vectors would allow veterinary authorities to develop more effective, science-based containment and preventative strategies against LSDV.

Further studies are required to investigate the role of vector saliva, the length of time in which mechanical vectors remain infective, the survival time of LSDV in their mouthparts or salivary glands, and the number of insects required to transmit infection.

Conflict of interest

The authors declare no conflict of interests.

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