Foot-and mouth disease and peste des petits ruminants – the role of wildlife in the epidemiology and control of diseases

WIESŁAW NIEDBALSKI, ANDRZEJ FITZNER, ANDRZEJ KĘSY

Department of Foot and Mouth Disease, National Veterinary Research Institute, Wodna 7, 98-220 Zduńska Wola, Poland

Niedbalski W., Fitzner A., Kęsy A.
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Summary

Foot-and mouth disease (FMD) and peste des petits ruminants (PPR) are highly contagious and an economically devastating diseases, currently endemic to the African and Asian continents. The aim of this paper was to present the role of wildlife in the epidemiology of both diseases. There are more than 100 species of wild, feral, laboratory, or domesticated animals that have been infected naturally or experimentally with FMD or PPR viruses. Experimental infections of several African wild ruminants can result in clinical FMD. African buffalo represents the best known FMD wild host reservoir in Sub-Saharan Africa. North American mule deer were found susceptible to FMDV infection with significant mortality. Other wild ruminants such as impala can also contribute to FMDV maintenance. In Europe several deer species and the Eurasian wild boar are susceptible to FMDV. PPRV has been reported to have infected some wildlife, such as African buffalo, saiga antelope, dorcas gazelles, gemsbok, Nubian ibex and some other ungulate species. The role of wildlife in FMD and PPR epidemiology may concern wildlife as indicators, victims, bridge hosts or maintenance hosts for both diseases. In addition, they are occasionally victims of disease outbreaks, and they are often relevant for disease management as either bridge or maintenance hosts. Wildlife deserves to become a key component of future integrated surveillance and disease control strategies in an ever-changing world. However, it must be stated that efforts to control FMD and PPR in wildlife may not be successful when the diseases are endemic in livestock and may cause more harm to wildlife, human livelihoods, and domestic animals.

Keywords: foot-and-mouth disease, peste des petits ruminants, wildlife, epidemiology, control

Foot-and mouth disease (FMD) and peste des petits ruminants (PPR) included in group of FMD and similar transboundary animal diseases (FAST diseases) are highly transmissible and have the potential for rapid spread regardless of national borders, causing serious socio-economic consequences. The prevention surveillance and contingency of these diseases are needed in non-endemic regions, including Europe. However, the role of wildlife hosts, has so far been neglected, therefore in this paper we present their role in the epidemiology of both highly contagious vesicular diseases of susceptible animals. These data can be useful for risk managers and decision-makers regarding wildlife-related aspects of disease prevention, surveillance, and contingency planning.

Foot-and-mouth disease

Foot-and-mouth disease (FMD) is the most highly contagious disease affecting livestock resulting in significant adverse economic impact worldwide (24). The disease is caused by infection with foot-and-mouth disease virus (FMDV), the prototypic member of the *Aphthovirus* genus within the family *Picornaviridae*. FMDV exists in seven distinct serotypes comprising O, A, C, Asia-1 and SAT 1-3 and multiple subtypes due to the high mutational rate of the virus. FMD is endemic in large areas of the continents of Africa and Asia. Viruses circulating in endemic regions are classified into seven separate endemic pools based on their antigenic and epidemiological properties (Fig. 1). The strict control on importation of animals and agricultural products allows Europe, North America and Australia to maintain a free status without vaccination. The EU protects itself procedurally from the introduction of FMD by implementing relevant legal regulations on infectious diseases. The new legal framework was provided by Regulation (EU) 2016/429 of the European Parliament and Council of March 9, 2016 on transmissible animal
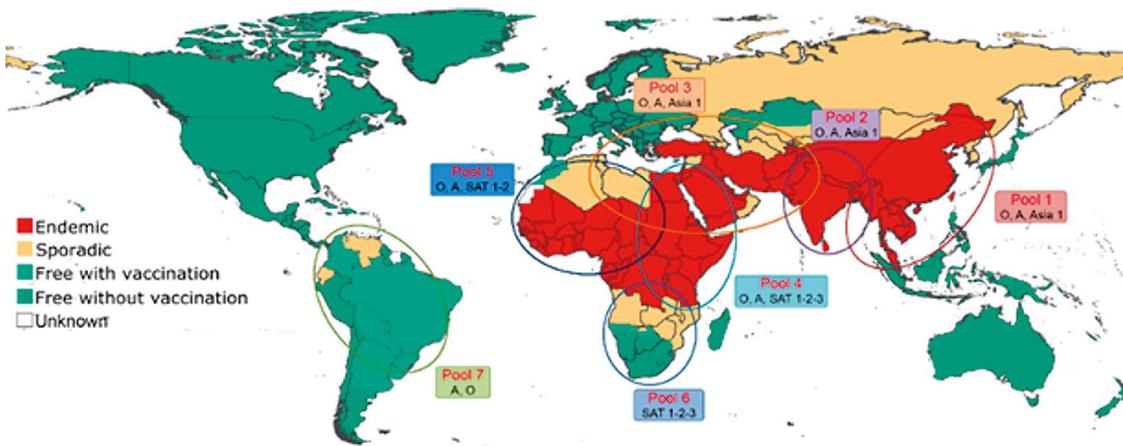
Fig. 1. Distribution of the seven endemic pools of FMDV showing global status of disease. According to WOAH/FAO Reference Laboratory Network for Foot-and-Mouth Disease (http://www.foot-and-mouth.org/)

diseases and amending and repealing certain acts in the area of animal health ("Animal Health Law"). Special control measures for FMD were applied in the EU as laid down rules in Commission Delegated Regulation (EU) 2020/687 of 17 December 2019 supplementing Regulation (EU) 2016/429 of the European Parliament and the Council, as regards rules for the prevention and control of certain listed diseased (http://data.europa.eu/eli/reg_del/2020/687/oj). These measures are based on stamping-out of infected and in-contact herds, and on regional restrictions on the movement of susceptible animals and their products. It is also important that the EU maintains one of the world's biggest antigen banks for express formulation of vaccines. Apart from domestic, over a hundred different wild animal species are susceptible to FMDV infection, either naturally or experimentally (44, 46, 52). Experimental infections of several African wild ruminants, as well as the African wild warthog (*Phacochoerus aethiopicus*) and bushpig (*Potamochoerus porcus*) can result in clinical FMD (27). African buffalo (*Syncerus caffer*) represents the best known FMD wild host reservoir in Sub-Saharan Africa (25). African Cape buffalo has been clearly shown to serve as long-term maintenance host (i.e. carrier) for the FMDV SAT serotypes, in population of Cape buffalo the virus has been estimated to persist for 24 years or longer. Infection in buffalo is subclinical and normally occurs in calves as soon as maternal antibodies wane at 2-6 months of age. Acutely infected buffalo provide sources of infection for other ruminants, both domestic and wild, directly or through other species which have contracted the infection from buffalo (9). Although the implication of the buffalo carriers in the epidemiology of FMD has not been fully clarified, they have so far been shown to transmit the disease while in that state (50). Phylogenetic relationships between SAT types FMDV strains isolated from cattle and those carried by buffalo have been reconstructed from different area of southern Africa, providing that contacts between livestock and buffalo regularly result in FMD outbreaks among cattle (10). Furthermore,

available evidence based on FMDV genome sequencing indicates that impala (*Aepyrecos melampus*) populations of the Kruger National Park – South Africa, usually become infected with SAT viruses derived from buffalo (19). Much is already know about the role that Cape buffalo plays in the FMD epidemiology, largely from studies conducted in South and East Africa; conversely, knowledge on the relationship between FMDV and wildlife and/or other buffalo subspecies that populate the rangelands of western and central African regions has been less through (14). Serosurveillance of FMDV in wildlife in Tanzania showed that 76.3% of tested buffalo sera samples were positive for FMDV using non-structure FMDV ELISA test for detection of antibodies directed against 3ABC non-structural proteins and confirming natural infection (34). The results of similar studies in wildlife species in Nigeria showed the 3ABC positive reactors in some waterbucks, wildebeests and elands and suggested that wildlife could equally play an important role in the overall epidemiology of FMD in Nigeria (7). North American mule deer (*Odocoileus hemionus*) were found susceptible to experimental FMDV infection with significant mortality and with deer-to-deer and deer-to-cattle transmission (46). Moreover, the susceptibility of bison (*Bison bison*) and elk (*Cervus elaphus nelson*) has been demonstrated after experimental by intraepithelial tongue inoculation infection with FMDV, strain O1 Manisa (45). Other wild ruminants such as impala (*Aepyceros melampus*) can also contribute to FMDV maintenance, at least locally and at certain densities (51). Also scimitar horned oryx (*Oryx dammah*), a large Sahelo-Saharan antelope, are susceptible to FMDV and highlight the risk of virus incursion into zoos and captive facilities in the Arabian Peninsula (31). The contact of some of these species, and notably of buffalo, with native cattle possesses disease transmission risks (13). In endemic regions, some wild hosts are susceptible to FMDV and can serve as disease indicators or, at some point, become victims, carriers, or maintenance hosts.

In late December 2010, FMDV was first confirmed from hoof lesions in a wild boar hunted in Bulgaria in a border region with Turkey (3). The outbreaks in domestic ungulates were controlled in the framework of EU legislation, including stamping out, standstill and no use of vaccination. All villages within the Cordon

Sanitaire were examined for the presence of FMD according to the control and eradication plan. Livestock outbreaks, 11 in total, were detected later, affecting cattle (*Bos taurus*), goats (*Capra aegagrus hircus*), sheep (*Ovis orientalis aries*) and pigs. In total, 2230 animals were culled by April 2011. This, along with a nationwide movement of restrictions on animals and their products, resolved the epidemic despite further sporadic FMD cases in wildlife, including roe deer (*Capreolus capreolus*) (3). Thus, in the UK and in Bulgaria, action on livestock facilitated FMD control without intervention on deer, wild boar or other wildlife. Hence, there is no empirical evidence in support of any claim that European wildlife can play a role in the maintenance of FMDV. In Europe, several deer species and the Eurasian wild boar (*Sus scrofa*) are susceptible to FMDV (22). Extensive surveillance in Bulgaria during their latest FMD outbreak determined that about 7% of 812 wild boar and 4% of 68 roe deer had antibodies against FMDV, but no viral RNA was detected. As expected by the authors, the relatively low seroprevalence and clustered spatial distribution of seropositive wild boar and roe deer suggest that the FMD infection in wildlife was mainly a short lived event which failed to develop into a large scale epidemic (3).

In contrast to Bulgaria, in 2001 in the Netherlands blood samples from 140 wild deer and 208 wild boar examined for antibodies to FMDV were all negative (19). While all susceptible species are relevant for active serosurveillance, those more prone to develop clinical FMD may be relevant for passive surveillance. The main wildlife species in Europe with records of clinical FMD are wild boar and roe deer (22), while experimental infection of red deer (*Cervus elaphus*) triggered only mild clinical signs (29). Options for wildlife FMD control include prevention (biosafety and movement control, including fencing), population control (targeted or random), and vaccination (18). Commercially available, inactivated FMDV vaccines have been used to effectively control FMD in many countries, and such vaccines have helped eliminate the disease from some areas of the world (42). These vaccines usually elicit high levels of neutralizing antibodies and offer efficacious protection against homologous FMDV serotypes (18). However, conventional inactivated FMD vaccines have a number of disadvantages, including incomplete inactivation of the virus, they do not induce broadly reactive long-term protection, require multiple vaccination to maintain good levels of immunity and require periodic inclusion of new viral strains into the vaccine formulation to cover new FMDV subtypes against which existing vaccines no longer protect. Other important shortcomings of conventional inactivated vaccines include short shelf life, the need for an adequate cold chain of formulated vaccines, and difficulties of certain FMDV serotypes and subtypes to grow well in cell cultures for vaccine production. Additionally, these vaccines do not

strictly have differentiation of infected from vaccinated animal (DIVA) characteristics (16). To overcome the shortcomings of inactivated vaccines, many efforts are currently devoted to developing novel FMD vaccines, including recombinant protein vaccines, synthetic peptide vaccines and empty capsid vaccines (36).

However, implementation of any of options for wildlife FMD control may not be 100% effective. For example, in FMD endemic regions of Africa, where FMDV circulates in livestock, buffalo, and possibly other wildlife, eradication is unlikely in the near future (52). Fencing is often used to separate wildlife from livestock, particularly in southern Africa, but has several disadvantages including cost and maintenance, as well as the disruption of natural movement of the wildlife population. In wildlife, stamping out is generally neither feasible nor desirable, and targeted culling of visibly diseased individuals is of little help if most infected individuals remain undetected (23). Combinations of fencing and cattle vaccination are in place, for instance around the Krüger National Park in South Africa (28). In endemic regions with wildlife reservoirs, improved livestock vaccination and improved husbandry in livestock, along with zonation and compartmentalization, might help in progressive disease control (40, 48). In Asia, saiga antelopes (*Saiga tatarica*) are susceptible to FMDV, and mortality due to FMD can be high. A decrease in FMD outbreaks in saiga occurred when surrounding cattle were vaccinated (52).

Peste des petits ruminants

Peste des petits ruminants (PPR) is a highly infectious viral disease of both domestic (goats and sheep) and wild ruminants (38). It is caused by the PPR virus (PPRV), a member of the genus *Morbilivirus* of the family *Paramyxoviridae* and is clinically and pathologically close to rinderpest (RP), measles virus (MV) in humans and canine distemper virus (CDV) (8). PPR was first recorded in early 1942 in the Ivory Coast, West Africa (30). In the next years the disease has extended its distribution in other parts of the world and is now circulating throughout Northern, Eastern and West Africa, Asia and Eurasia, the Indian subcontinent, and the Middle East. It is spreading globally, with emergence notably reported in China, Mongolia, the Indian subcontinent, Pakistan, Afghanistan, Iran, Iraq, Saudi Arabia and Turkey (www.fao.org/3/a-i4460e.pdf), and recently within the European Union in Bulgaria where PPR outbreak was reported on June 24, 2018 in the village of Voden, Bolyarovo municipality of Yambol region, on the border with the Thrace region of Turkey (4). Due to the devastating effect of PPR on livestock and livelihoods, the Food and Agriculture Organization of the United Nations (FAO) and the World Organization for Animal Health (WOAH) endorsed the Global Strategy for the Control and Eradication of PPR (PPR GCES), and launched

the PPR Global Eradication Programme (PPR GEP), to eradicate the disease by 2030.

In Asia a wide range of wild cloven-hoofed animals are susceptible to PPRV infection. This has been confirmed on the basis of the results of serological tests and samples from clinical disease outbreaks using molecular methods. In most of these cases, it is likely that there was spillover of the virus from nearby populations of infected domestic small ruminants leading to sporadic wildlife epidemics and possible cross-species transmission between wild species (35, 41). Many wild artiodactyls including ovines, caprines, bovines and gazelles have been found naturally infected, mainly in Asia (21). In Africa, the only reports of antigenic or molecular confirmation of PPR disease in wildlife species to date were in Sudan (6, 41). This is surprising, considering the large populations of PPRV susceptible wild species in Africa, and needs further investigation. It is possible that PPR disease has occurred in other free-ranging wild species in other regions in Africa, but has not been detected or has not been reported because of the remoteness of wild populations, limited capacity for wild animal disease surveillance and the fact that sick or dead wild animals could be removed by predators and scavengers before they are identified. The reports of PPR from Sudan were in Nile lechwe (*Kobus megaceros*) in 2008, and in dorcas gazelles (*Gazelle dorcas*) in 2016-2017, but the clinical, pathological, epidemiological and laboratory details related to these reports are incomplete, so there is uncertainty about the occurrence of naturally occurring PPR in these wild populations (6, 41). PPR outbreaks have decimated endangered wildlife populations, as it was in case of the saiga antelope in Mongolia (40). Caprinae are especially sensitive to PPRV, which causes high mortality in wild caprines and ovines. For example, an approximate quantification of the die-offs in wild goats (*Capra aegagrus*) has been estimated at 25-77% (33). In endemic regions, wildlife does not appear to maintain PPRV infection (32). White-tailed deer (*Odocoileus virginianus*) have been experimentally infected, further expanding the range of susceptible hosts (26). However, due to our still incomplete understanding of PPR in wildlife and considering that wildlife may act as bridge hosts (12), the role of wildlife in PPR epidemiology and control cannot be ignored (21). Few ecosystems in the world have large enough populations of wild species for the potential maintenance of PPR in wildlife: for example, eastern Mongolia, the Boma-Gambela ecosystem in South Sudan and Ethiopia, and the Greater Serengeti ecosystem in Kenia and Tanzania. A broad wild-domestic interface exists around unfenced natural areas and effective contacts for pathogen transmission increasingly occur between livestock and wildlife. PPRV spreading from a domestic source was suggested in the Serengeti ecosystem in Tanzania with higher antibody prevalence in wildlife close to livestock, but without clinical syndromes or mortality (32). Nevertheless it is becoming clearer as to the role of wildlife in PPR epidemiology, with most data supporting the hypothesis of wildlife as a victim rather than reservoir (32, 40). Recent progress in PPR eradication suggests that at least in settings with low wildlife densities wildlife does not significantly interfere with PPR control (2). Several European wildlife species, certain ibex species and probably some deer species, also can get infected (1, 26). These species are not in danger but contact with small ruminants does occur. Thus, wildlife could potentially contribute to PPRV maintenance in multi-host settings if it entered Europe, or at least act as bridge hosts, although the risk is possibly low. Multiple wildlife species can be infected with PPRV and might therefore serve as indicators (15). Existing knowledge gaps hinder a functional PPR surveillance system that includes wildlife surveillance as mentioned in the FAO/OIE Global Eradication Programme of PPR by many countries (21). With the current state of knowledge, wildlife should be considered at least as indicator species, in regional holistic (integrated) surveillance schemes (11). Attempts to protect valuable wildlife hosts have included vaccination of captive collections (47).

Wildlife and disease surveillance

Wildlife disease surveillance can contribute to the early detection of FMD. This was the case in the Bulgarian FMD outbreak in 2011, where the first diagnosed FMD case was in hunted wild boar presenting FMD-compatible lesions (3). One of the disadvantages of working with wildlife is the generally more difficult access to individuals for sampling or treatment as compared to livestock. However, this eventually becomes an advantage for disease surveillance in regions where suitable domestic hosts are vaccinated and non-vaccinated wildlife species can act as indicators of pathogen circulation (43). For instance, the current PPR control initiative aims at protecting sheep and goats through blanket vaccination (53). Under these circumstanced, detecting PPR or antibodies against PPRV in young animals and wild ruminants would help to identify areas with PPRV circulation (20). Fine at all. (21) recommended establishing and sharing clear guidelines and standards for PPR diagnosis in wildlife and maintaining appropriate wildlife disease surveillance schemes. In outbreak regions, active disease surveillance, for instance on hunter-harvested wild ungulates, might help to confirm disease absence. However, wildlife disease surveillance is challenging in distant regions. Filter paper can be useful for safe and convenient blood and nucleic acid sampling from wildlife in remote regions (49). Fresh fecal samples can be used for non-invasive sampling and PCR testing for FMD and PPR. In the laboratory, competitive ELISA assays can avoid the lack of species-specific antibodies in wildlife (15), and antigen detection tests are host species independent. In addition to the role of

wildlife as indicators of FMDV and PPRV circulation, wildlife can be bridge hosts or even maintenance hosts for some infections, eventually also becoming victims with substantial mortality or negative effects in their populations. If this is the case, highly susceptible wildlife species can also contribute to early disease detection. However, their role varies regionally and is dynamic.

The effect of FMD and PPR on wildlife populations is largely unknown, and only the case of PPRV and saiga antelopes is sufficiently documented (40). In the case of FMD, the bridge-host role of wildlife such as wild boar is well-established (3). Considering the huge diversity and changing range and dynamics of wildlife hosts, and the ongoing expansion and increasing diversity of animal diseases, it is advisable to always expect the unexpected (5). Recently, interesting data supporting the susceptibility of white-tailed deer to SARS-CoV-2 have been presented (37). These examples showcase the endless unexpected links between wildlife, livestock, and human health and well-being. Similar unexpected interactions might happen anytime in any region, host and pathogen. Therefore, wildlife deserves to become a key component of future integrated surveillance and disease control strategies in an ever-changing world. It is advisable to improve our knowledge on wildlife implications in FMD and PPR. This will improve our preparedness for the case when an outbreak occurs in formerly disease-free regions where wildlife may be relevant for disease surveillance and control.

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Corresponding author: Wiesław Niedbalski, PhD, DSc, Wodna 7, 98-220 Zduńska Wola, Poland; e-mail: wieslaw.niedbalski @piwzp.pl