

REVIEW

Open Access



Airborne transmission of common swine viruses

Zhiqiang Hu^{1,3,4,5†}, Xiaogang Tian^{1,3,4†}, Ranran Lai^{1,3,4}, Chongxing Ji^{2,3} and Xiaowen Li^{1,2,3,4,5*}

Abstract

The transmission of viral aerosols poses a vulnerable aspect in the biosecurity measures aimed at preventing and controlling swine virus in pig production. Consequently, comprehending and mitigating the spread of aerosols holds paramount significance for the overall well-being of pig populations. This paper offers a comprehensive review of transmission characteristics, influential factors and preventive strategies of common swine viral aerosols. Firstly, certain viruses such as foot-and-mouth disease virus (FMDV), porcine reproductive and respiratory syndrome virus (PRRSV), influenza A viruses (IAV), porcine epidemic diarrhea virus (PEDV) and pseudorabies virus (PRV) have the potential to be transmitted over long distances (exceeding 150 m) through aerosols, thereby posing a substantial risk primarily to inter-farm transmission. Additionally, other viruses like classical swine fever virus (CSFV) and African swine fever virus (ASFV) can be transmitted over short distances (ranging from 0 to 150 m) through aerosols, posing a threat primarily to intra-farm transmission. Secondly, various significant factors, including aerosol particle sizes, viral strains, the host sensitivity to viruses, weather conditions, geographical conditions, as well as environmental conditions, exert a considerable influence on the transmission of viral aerosols. Researches on these factors serve as a foundation for the development of strategies to combat viral aerosol transmission in pig farms. Finally, we propose several preventive and control strategies that can be implemented in pig farms, primarily encompassing the implementation of early warning models, viral aerosol detection, and air pretreatment. This comprehensive review aims to provide a valuable reference for the formulation of efficient measures targeted at mitigating the transmission of viral aerosols among swine populations.

Keywords Aerosol, Swine virus, Transmission distance, Experimental condition, Field condition, Influential factors, Preventive strategy

[†]Zhiqiang Hu and Xiaogang Tian have contributed equally to this work.

*Correspondence:

Xiaowen Li

lxw8272@163.com

¹ Shandong Engineering Laboratory of Pig and Poultry Healthy Breeding and Disease Diagnosis Technology, Xiaojin New Hope Liuhe Agriculture and Animal Husbandry Co., Ltd, Xiaojin Economic Development Zone, Qingwo Venture Park, Dezhou 253200, Shandong Province, People's Republic of China

² Key Laboratory of Feed and Livestock and Poultry Products Quality and Safety Control, Ministry of Agriculture and Rural Affairs, New Hope Liuhe Co., Ltd, 316 Jinshi Road, Chengdu 610100, Sichuan, People's Republic of China

³ Shandong New Hope Liuhe Co., Ltd, No. 592-26 Jiushui East Road Laoshan District, Qingdao 266100, Shandong, People's Republic of China

⁴ Shandong New Hope Liuhe Agriculture and Animal Husbandry Technology Co., Ltd (NHLH Academy of Swine Research), 6596 Dongfanghong East Road, Yuanqiao Town, Dezhou 253000, Shandong, People's Republic of China

⁵ China Agriculture Research System-Yangling Comprehensive Test Station, Intersection of Changqing Road and Park Road 1, Yangling District, Xianyang, People's Republic of China



Background

The significance of biosecurity in farms is increasingly acknowledged due to the significant challenges posed by the ASFV to the global pig industry, particularly in Asia, where conventional interventions such as vaccines or drugs have proven ineffective in addressing these issues [1, 2]. In the biosecurity system, aerosol transmission has always been a weak link in biosecurity prevention and control, thus understanding and preventing aerosols is extremely important for the health of pig populations. The investigation of aerosol transmission is a specialized and noteworthy area of study, particularly in relation to the examination of swine viral aerosols. In a previous review, STARK [3] presented a comprehensive overview of pathogen aerosols in pig farms, offering valuable and enduring perspectives that continue to be cited and employed by farmers, despite the passage of time. However, recent advancements in research techniques and the growing needs of farmers have led to the identification of additional aerosol-borne viruses and the revelation of more intricate transmission patterns.

Bioaerosols, characterized by the presence of small droplets or particles measuring less than 5 μm suspended in a gaseous medium, possess the capacity to transport pathogenic microorganisms and facilitate the transmission of diseases [4]. The present review is specifically

dedicated to viral aerosols laden with swine viruses. Respiratory activity in swine populations serves as a notable origin of aerosols [5]. Pathogenic viruses can be actively or passively released into the air via aerosols, resulting in extensive dissemination of the virus [6–8]. The potential of viral aerosols to induce diseases is primarily contingent upon the infectivity of the pathogen and the requisite dosage for a susceptible host [9]. The dynamics and dispersion of viral aerosols are influenced by a multitude of factors, including aerosol diameter, initial velocity, temperature, relative humidity, ultraviolet radiation, airflow, ventilation, and filtration [10–12]. The viability of viruses within aerosols is impacted by the initial metabolic state of the virus, genetic characteristics, and the surrounding environment.

This review comprehensively summarizes the latest characteristics of aerosol transmission for various common swine viruses (Table 1), including FMDV, PRRSV, IAV, PEDV, PRV, CSFV, ASFV, porcine circovirus (PCV), swine vesicular disease virus (SVDV), Japanese encephalitis virus (JEV), and porcine respiratory coronavirus (PRCV). Notably, it encompasses a summary of several recently discovered viruses that exhibit the ability to be transmitted via aerosols, including SIV, JEV, PCV, and PEDV. Additionally, by drawing upon practical experiences and strategies employed in the prevention

Table 1 Characteristics and influential factors of aerosol transmission for different swine viruses

Category	Virus	Diameter (nm)	Distance of transmission	Viral loads in aerosols	Experimental evidence	Field evidence	Influential factors
Long-distance	FMDV	26	300 km [18, 19]	$10^{5.8}$ – $10^{6.4}$ TCID ₅₀ [24]	Yes [24]	Yes [17, 19]	Viral strain, host species, weather condition, geographical condition, environmental condition, contract structure
	PRRSV	60	9.2 km [30]	6×10^2 – 5.1×10^4 copies / m ³ [35]	Yes [28, 29]	Yes [30]	Viral strain, mixed pathogen, aerosol particle size, environmental condition
	IAV	80–120	2.1 km [40]	10^4 – 10^7 copies/m ³ [39]	Yes [41]	Yes [40]	Viral strain, aerosol particle size, environmental condition,
	PEDV	95–190	16.1 km [51]	1.3×10^6 – 3.5×10^8 copies/ m ³ [35]	Yes [54]	Yes [51]	Viral strain, aerosol particle size, wind direction, age of susceptible animals
	PRV	225	13.8 km [60]	$10^{5.3}$ TCID ₅₀ [59]	Yes [59]	Yes [60]	Unknown
Short-distance	CSFV	40–50	1 m [65]	$10^{1.2}$ – $10^{3.8}$ TCID ₅₀ /m ³ [70]	Yes [65]	Yes [64]	Viral strain, viral dose, RH, wind speed
	ASFV	200	10 m [78]	$10^{3.2}$ TCID ₅₀ /m ³ [81]	Yes [76, 77]	Yes [78]	Unknown
Others	PCV	17	Unknown	10^7 copies/m ³ [84]	Unknown	Yes [84]	Unknown
	SVDV	24–26	Unknown	$10^{1.4}$ – $10^{2.6}$ TCID ₅₀ [89]	Unknown	Yes [89]	Unknown
	JEV	50	Unknown	Unknown	Yes [97]	Unknown	Unknown
	PRCV	100–160	Unknown	$10^{1.87}$ PFU/m ³ [104]	Yes [105]	Unknown	Unknown

and control of human aerosol-transmitted viruses, we propose innovative approaches that hold potential for application in the prevention and control of aerosol transmission within pig production. This review is expected to serve as a valuable reference for the formulation of effective strategies to prevent the transmission of viral aerosols among pig populations.

Airborne swine viruses in pigs

In this section, we summarize the characteristics and influential factors of aerosol transmission of various prevalent swine viruses. The transmission distance of viral aerosols holds significant importance, as evidenced by a scholarly report suggesting that a spatial separation exceeding 150 m between structures can effectively mitigate the risks associated with airborne transmission [3]. Consequently, we classify these viruses into three distinct categories based on their respective aerosol transmission distances (Table 1): long-distance transmission viruses (exceeding 150 m), short-distance transmission viruses (ranging from 0 to 150 m), and other viruses with unknown transmission distances. The long-distance transmission viruses primarily occur between farms, while the short-distance transmission viruses mainly occur within a farm.

Long-distance airborne viruses

FMDV

FMDV, belonging to the *Aphthovirus* genus within the *Picornaviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 26 nm. It primarily causes vesicular diseases affecting the oral mucosa, hoof parts, and udder skin in pigs, cattle, and sheep, which is also a zoonotic disease [13]. The airborne transmission of FMDV under field conditions has been extensively investigated, with a particular focus on the creation of mathematical models that incorporate variables such as meteorological conditions and wind patterns [14–16]. These models have greatly expanded our understanding of the characteristics of FMDV airborne transmission. Hugh-Jones' report indicates that aerosol transmission of FMDV on land can reach distances of 60–150 km with the assistance of favorable weather conditions, including wind and rain [17]. Moreover, the transportation of viruses over long distances through plumes is particularly probable across seaways due to the minimal surface turbulence and the ability to sustain airborne particle concentrations for greater distances compared to land areas [18]. It is believed that the farthest distance of airborne dissemination over the sea is approximately 300 km, from pig farms experiencing FMDV outbreaks in Brittany (northern France) to cattle farms located on the Isle of

Wight [14, 17, 19]. Consequently, the capacity for FMDV to transmit through the air is influenced by both weather conditions and geographical factors. Another important factor is that susceptibility to the virus varies among different species, with ruminants becoming infected with as little as 10 TCID₅₀ dose, whereas pigs require a dose of 6×10^3 TCID₅₀ [20, 21]. And the shed virus in saliva and nasal swabs from FMDV-infected pigs is 100–1000 times more infectious for sheep and cattle than the minimum infectious dose, indicating the potential role of pigs as an important source for airborne transmission [22, 23]. An integrated model developed by SÉRENSEN et al. showed that when 1,000 pigs were infected and released the virus, the longest airborne distances for downwind cattle, sheep and pigs were 300 km, 90 km and 20 km, respectively, which also supports the above opinion [15]. Under experimental conditions, more details about aerosol propagation signatures of FMDV were discovered. In a study by Alexandersen et al., three strains of FMDV in aerosols showed that each pig could release $10^{5.8}$ – $10^{6.4}$ TCID₅₀ of the virus into the air within a 24-h period [24]. Eble et al. conducted a study and found that the estimated between-pen transmission rate of FMDV was 0.59 per day, while the within-pen transmission rate was 6.14. This suggests that the contact structure between pigs significantly influences the transmission rate of FMDV [25]. Furthermore, it has been observed that FMDV has a greater likelihood of survival in environments with temperatures below 60 °C, relative humidity (RH) above 55%, and a neutral pH. This indicates that environmental factors may also have a significant impact on the airborne transmission of FMDV [26].

PRRSV

PRRSV, belonging to the *Arterivirus* genus within the *Arteriviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 60 nm. It primarily causes reproductive disorders in sows and respiratory difficulties in piglets [27]. Research has demonstrated that PRRSV can be transmitted through aerosols with a range of 0.5–150 m under experimental conditions [28, 29], whereas the distance can extend up to 9.2 km or even further under field conditions [30]. The primary factors effecting the airborne transmission capacity of PRRSV are viral strains and mixed pathogens. On the one hand, Torremorell et al. found that the PRRSV strain VR-2332 could be transmitted through the air, while highly pathogenic field strains (MN-1b) could not [31]. Research conducted by Cho et al. also demonstrated that the pathogenicity of PRRSV isolates significantly affects the frequency of aerosol shedding but does not significantly influence the concentration of the virus in aerosols [32, 33]. On

the other hand, Otake et al. demonstrated that airborne transmission only occurred under mixed conditions with PRRSV variants 1-8-4 and porcine pneumonia-associated *Mycoplasma hyopneumoniae* (MHYO) 232, and the air samples collected at a distance of 9.2 km from the pig population remained infectious [30]. Additionally, Brockmeier et al. reported that pigs co-infected with PRRSV and *Actinobacillus pleuropneumoniae* exhibited an increased frequency and duration of sneezing and coughing, indicating a higher potential for aerosol transmission of pathogens [34]. Other important factors are aerosol particle sizes and environmental conditions. Alonso et al. demonstrated that the concentration of PRRSV viral particles in aerosols with different diameters range from 6×10^2 (0.4–0.7 μm) to 5.1×10^4 (9.0–10.0 μm) copies/ m^3 [35]. The half-life of PRRSV in aerosols is less than 30 min at a temperature of 30 °C, and low RH conditions favor the survival of the virus in aerosols [2, 36], which is the basis for developing measures for virus aerosol disinfection in farms.

IAV

IAV, belonging to the *Influenza A* genus within the *Orthomyxoviridae* family, is an enveloped single-stranded negative-sense RNA virus with a diameter of 80–120 nm. It primarily causes a zoonotic respiratory disease characterized by coughing, respiratory distress, and fever [37]. The airborne transmission has been detected under both experimental conditions and field conditions. Under field conditions, a study revealed that 71% of the 122 bio-aerosol samples collected from large-scale farms tested positive for IAV [38]. And, IAV was isolated from indoor aerosol samples of a commercial pig farm, with the highest viral loads observed 7–11 days after an outbreak (10^4 – 10^7 copies/ m^3), persisting for 20 days [39]. Furthermore, IAV has been isolated from air samples collected both inside and outside pig farms [40], indicating the risk of airborne transmission between farms. Further studies showed that the transmission distance has been observed to be up to 2.1 km downwind [40]. Under experimental conditions, Zhang et al. demonstrated IAV of S-O 2009 IV strain was able to be aerosolized by infected animals and to be transmitted to susceptible animals by airborne routes in pig and guinea infection models, and the airborne distance was a range of 2.0–4.2 m [41].

There is a limited amount of literature available regarding the aerosol transmission factors impacting swine influenza virus. Nevertheless, there exists a substantial body of research on other species that can be utilized as a point of reference. The primary factors influencing the capacity of IAV airborne transmission are viral strains, environmental conditions, and sizes of aerosol particles. Mubareka et al. [42] discovered notable variations in the

aerosol transmission capacity among different strains of IAV, and subsequent investigations have confirmed that these differences can be attributed to amino acid mutations in the neuraminidase and hemagglutinin gene of different IAV strains, which can affect the affinities between virus and receptors of different hosts and viral replication ability in the respiratory tract [43–45]. Environmental conditions influence airborne transmission mainly by RH and ambient air temperature [46]. Under field conditions, research has also found that environmental conditions with a RH of 20–35% and a temperature of 5 °C are most favorable for IAV transmission [47]. Furthermore, Lindsley et al. [48] conducted a study employing a human cough model, which revealed the presence of IAV RNA in aerosol particles of various sizes. The findings indicated that 35% of the RNA was detected in particles larger than 4 μm , 23% in particles ranging from 1 to 4 μm , and 42% in particles smaller than 1 μm . These particles fell within the respirable size range.

PEDV

PEDV, belonging to the *Coronavirus* genus within the *Coronaviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 95–190 nm. It primarily causes severe enteric diseases with high mortality and watery diarrhea in 7-day-old piglets [49, 50]. Aerosol transmission of PEDV has been observed up to a distance of 16.1 km under field conditions, as first detected by Alonso et al. in infectious viral particles in aerosol samples from PEDV-positive pig herds [51]. The aerosol transmission of PEDV is primarily related to aerosol particle size, viral strains, wind direction, and the age of susceptible animals [52]. PEDV can be detected in aerosol particles across all diameter ranges, with the contents from 1.3×10^6 (0.4–0.7 μm) to 3.5×10^8 (9.0–10.0 μm) copies/ m^3 , and the aerosols with viral particles can survive in the environment for up to 9 months [35, 53]. Research by Gallien et al. showed that under experimental conditions, non-InDel PEDV strains exhibited earlier detection and higher viral loads in the air under experimental conditions, indicating a higher efficiency of aerosol transmission [54]. Furthermore, Beam et al. utilized geospatial methods and meteorological data to establish a correlation between wind direction and the aerosol transmission of PEDV [55]. Li's research provided evidence of pre-weaning piglets being infected with PEDV through viral aerosols, as intranasal administration of 1 mL of wild-type PEDV (10^7 PFU/mL) resulted in typical PED symptoms in 5-day-old piglets [56]. However, Niederwerder et al. found that aerosols generated from PEDV-inoculated animals did not cause disease in 4-week-old piglets, suggesting that pigs of different ages may have varying tolerance to viral aerosols [57].

PRV

PRV, belonging to the *Varicellovirus* genus within the *Herpesviridae* family, is an enveloped double-stranded DNA virus with a diameter of approximately 225 nm. It primarily causes an acute infectious disease characterized by high fever, abortion, and neurological symptoms not only in pigs, domestic livestock, and various wild animals [58]. Donaldson et al. conducted an experiment under experimental conditions wherein healthy pigs in one pen were effectively infected through exposure to aerosols emitted by PRV-positive pigs housed in another pen, connected by a pipe [59]. Each PRV-positive pig released virus particles into the air, with peak titers reaching a maximum of $10^{5.3}$ TCID₅₀ within 24 h [59]. Grant et al. further substantiated the aerosol transmission of PRV through the utilization of a Gaussian diffusion model [60]. Under field conditions, aerosols containing PRV can be dispersed by the wind, reaching distances ranging from 1.3 to 13.8 km or even more [60–62]. However, there is currently a lack of in-depth study on the airborne transmission of PRV.

Short-distance airborne viruses

CSFV

CSFV, belonging to the genus *Pestivirus* within the *Flaviviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of 24–26 nm. It mainly causes acute fever and bleeding in pigs [63]. A study by Elbers et al. analyzed factors related to the field transmission of CSFV and suggested airborne transmission as one of the most important routes of infection [64]. Gonzalez et al. demonstrated that CSFV can be transmitted through aerosols in non-contact situations under an experimental condition, with a transmission distance of up to 1 m. The main factors affecting airborne transmission of CSFV include RH, wind speed, viral dose, and viral strains [65]. Lu et al. confirmed that low relative humidity and high wind speed are important factors contributing to CSFV outbreaks, as they promote the widespread dissemination of aerosols [66]. Two studies by Laevens et al. showed that CSFV was only transmitted through aerosols to other pig pens after all the pigs in the infected pen have become ill, suggesting that a certain level of viral loads is required for aerosol transmission [67, 68]. Weesendorp et al. found that airborne transmission played an important role in the later stage of CSF outbreaks, which aligns with Laevens' conclusions [69]. Additionally, Weesendorp et al. further studied the airborne transmission of different CSFV strains with varying virulence and found that strains with higher viral concentrations or higher virulence were associated with higher viral loads in aerosol samples, ranging from $10^{1.2}$ to $10^{3.0}$ TCID₅₀/m³ (moderate virulence) to $10^{1.6}$ – $10^{3.8}$

TCID₅₀/m³ (high virulence) [70]. Moreover, research has shown that CSFV remains infectious in an aerosolized state for at least 30 min, with a half-life ranging from 4.5 to 15 min [71].

ASFV

ASFV, belonging to the *Asfivirus* genus within the *Asfarviridae* family, is an enveloped double-stranded DNA virus with a diameter of approximately 200 nm. It is also the only known DNA arthropod-borne virus [72, 73]. ASFV primarily causes an acute, hemorrhagic, highly contagious disease in domestic and wild pigs, with a mortality rate of up to 100% [74, 75]. Wilkinson et al. demonstrated that ASFV can be transmitted by aerosols from ASFV African strains-positive pigs, with a potential distance infecting up to 2.3 m, providing initial evidence of airborne transmission of ASFV under experiment conditions [76]. European ASFV strains were also shown to spread through aerosols among pigs through aerosols, infecting healthy pigs in separate pens [77]. According to the latest research by Li et al., the transmission distance of ASFV Asian strains under field conditions can reach up to 10 m [78]. And secretions carrying high viral titers from ASFV-positive pigs during sneezing and coughing can be aerosolized and emitted into the environment [79, 80]. Under experimental conditions, the half-life of ASFV in aerosols was approximately 14 min, with viral titers up to $10^{3.2}$ TCID₅₀/m³ found in aerosol samples collected from rooms with ASFV-positive pigs [81]. The prevention of aerosol transmission of ASFV constitutes a crucial component of prevailing biosecurity systems implemented in numerous pig farming operations. Regrettably, the present body of research on the mechanism, determinants, and preventive strategies pertaining to aerosol transmission remains insufficient. Given the persistent threat posed by ASFV to the worldwide swine industry, it is imperative that this area be urgently explored through future investigations.

Other viruses with unknown transmission distances

PCV

PCV, belonging to the *Circovirus* genus within the *Circoviridae* family, is a non-enveloped single-stranded DNA virus with a diameter of approximately 17 nm. It primarily targets and impairs the immune system of susceptible animals [82, 83]. Verreault et al. discovered the presence of PCV2 in the air of pig barns, with a concentration of 10^7 copies/m³ [84]. Another study also detected PCV2-positive aerosol samples in pig farms and slaughterhouses [85]. Additionally, PCV2 was found in nasal lavage samples from farmers (4/78) working in a pig farm, indicating a high risk of PCV2 transmission through aerosols [86]. However, the transmission distance and the precise

mechanisms of aerosol transmission of PCV2 are not yet clear.

SVDV

SVDV, belonging to the *Enterovirus* genus within the *Picornaviridae* family, is a non-enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 24–26 nm. It primarily causes vesicular diseases affecting the hooves, oral cavity, nostrils, and mammary glands in pigs [87, 88]. Under field conditions, Sellers et al. collected aerosol samples from SVDV-positive pig herds and detected SVDV viral particles in aerosols of different particle sizes, ranging from $10^{1.4}$ TCID50 ($<3 \mu\text{m}$) to $10^{2.6}$ TCID50 ($>6 \mu\text{m}$) [89]. SVDV viral particles were also found in the noses of farmers who had been in contact with pigs for more than 5 min, with viral titers approximately $10^{2.4}$ TCID50 [89]. It is suspected that the main source of aerosols containing SVDV is the shedding of virus particles from ruptured lesions which subsequently form aerosols, leading to rapid transmission [90]. And SVDV can be detected in aerosols within 2–3 days after infection, with viral loads being 160 times lower than those of FMDV [23, 91]. However, there is currently a lack of in-depth study on the airborne transmission of PRV.

JEV

JEV, belonging to the *Flavivirus* genus within the *Flaviviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 45–50 nm. It primarily causes a zoonotic disease characterized by high fever and neurological symptoms [92]. JEV transmission has been exclusively described as being mosquito-mediated. However, studies have shown that the nasal mucosa serves as an entry and exit route for the virus [93, 94]. In an animal experiment, the average virus titer in the nasal secretions of infected pigs was 2.25×10^2 TCID50/mL [95], and even a low virus titer of 10 TCID50/mL successfully infected pigs through the intranasal route [96]. The aforementioned findings suggest that pigs are susceptible to infection by aerosols carrying JEV. Thus far, only one study has provided evidence of aerosol transmission of JEV between mice under experimental conditions [97].

PRCV

PRCV, belonging to the *Coronavirus* genus within the *Coronaviridae* family, is an enveloped, single-stranded positive-sense RNA virus with a diameter of approximately 100–160 nm. It is a natural deletion mutant of the enteropathogenic TGEV [98–100]. PRCV primarily causes subclinical respiratory symptoms, such as mild bronchio-interstitial pneumonia and neutrophil

infiltration [101, 102]. Costantini et al. have demonstrated that PRCV can replicate in the respiratory tracts of pigs and be transmitted through aerosols, infecting pigs of any age through contact or airborne transmission [103]. Research by Bourgueil et al. in experimental conditions also demonstrated that air samples from pig pens with PRCV-positive pigs remained positive for 6 days, with the highest level reaching $10^{1.87}$ PFU/m³ [104]. Cox et al. aerosolized solutions containing the PRCV-TLM83 strain at a concentration of 10^7 TCID50, and successfully infected 1-week-old piglets by inoculating them with the collected aerosols [105]. Another research by Keep et al. indicated that there was no difference of viral load detection and pathology in respiratory tissues of PRCV-infected pigs with two different infection routes, aerosol and intranasal/tracheal, which indicating a high sensitivity of PRCV-positive aerosols by pigs [106]. It is worth noting that PRCV is highly sensitive to environmental factors and can only be sustained under specific conditions, namely 47% relative humidity and a temperature of 20 °C [107]. Currently, there is a lack of research on the transmission distance and other comprehensive investigations of PRCV aerosols.

Above all, the primary evidence concerning the transmission of viral aerosols is derived from field and laboratory studies. Detecting aerosol transmission under field conditions, especially in the early stages, poses significant challenges. Mathematical models based on epidemiological surveys and case reports play a crucial role in understanding long-distance virus transmission and the emergence of new viruses. Extensive research has been conducted on the utilization of mathematical models in the context of FMDV [14–16], and this approach can be further applied to the investigation of other virus aerosols. Moreover, recent comprehensive case reports and source tracing analyses pertaining to the aerosol transmission of ASFV [78] and COVID-19 [108] have yielded exemplary demonstrations. Consequently, more case reports on the aerosol transmission of viruses should be encouraged in the future. Furthermore, the transmission of viral aerosols in pig farms is significantly influenced by several key factors, including aerosol particle sizes, viral strains, the host sensitivity to viruses, weather conditions, geographical conditions and environmental conditions, which supply basis for the development against viral aerosols in pig farms.

Prevention of airborne viruses in pig farms

Airborne transmission plays a pivotal role in the containment of animal diseases and is equally significant in the dissemination of zoonotic diseases. Consequently, it is imperative to prioritize endeavors aimed at preventing airborne transmission. However, given

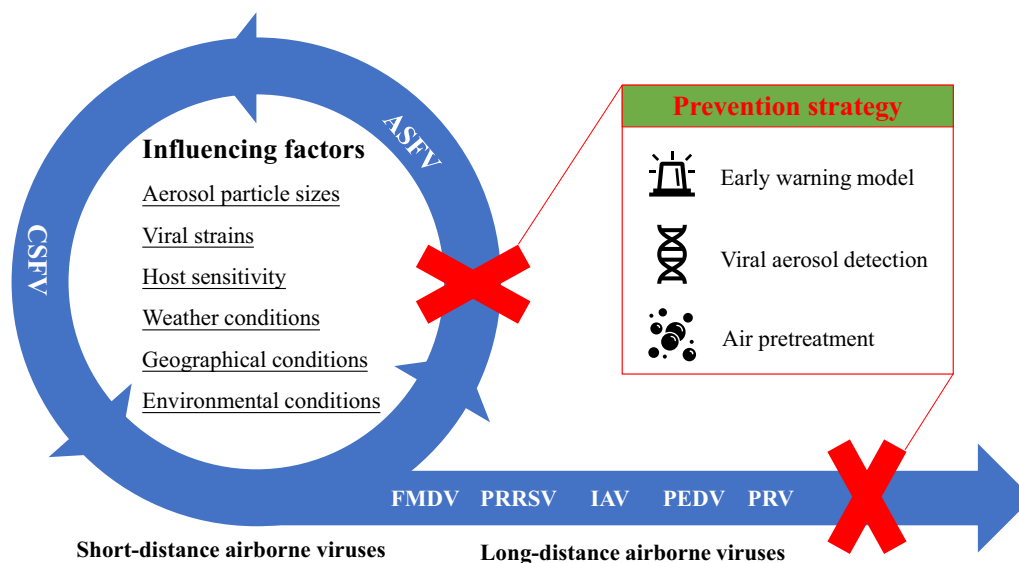


Fig. 1 Schematic diagram of aerosol transmission and prevention for swine viruses

the scarcity of research on the prevention of aerosol transmission in pig farms and the current reliance on relatively simplistic preventive measures, here, we propose integrating insights from studies on viral aerosol transmission diseases in humans to propose potential preventive and control strategies that could be implemented in pig farms.

Establishment of early warning models

The implementation of a real-time early warning monitoring system or regional risk maps for viral aerosol transmission is crucial for disease prevention, control and the improvement of biosecurity measures for pig farms. The establishment of an early warning model for West Nile virus provides a valuable reference [109]. Firstly, it is important to note that the long-distance transmission of most aerosol-borne diseases, such as FMDV [17, 19] and PEDV [55], is strongly influenced by climate and geographical factors, as previously mentioned. Hence, climate factors including temperature, humidity, precipitation, wind speed, and wind direction, as well as geographical factors such as altitude and terrain, should be included as parameters within this model. Secondly, the inclusion of epidemiological investigation data pertaining to previous viral diseases within a particular region is crucial. Lastly, it is imperative to incorporate routine pathogen monitoring data pertaining to personnel, drinking water, wastewater, feed, and manure in pig farms as variables in this model, as they can serve as indicators for evaluating the extent of environmental contamination in a specific locality. For example, Silva’s report highlights the significance of wastewater monitoring in enhancing the early warning surveillance of SARS-CoV-2 transmission [110]. By collecting the

forementioned parameters, an early warning model can be established, which represents interdisciplinary research that holds significant implications for the pig farming industry.

Detection of viral aerosols

Monitoring viral aerosols in pig farms can function as a proactive measure to mitigate airborne transmission [111]. However, the efficacy of air sampling and pathogen detection is significantly diminished under field conditions due to high gas exchange rates. Consequently, enhancing the sensitivity of detection methods and the collection efficiency of air samplers can enhance the likelihood of identifying viral aerosols during the early stages of transmission. Given the escalating threat of ASFV to pig production, numerous detection methods for swine viruses with high sensitivity have been devised, such as digital polymerase chain reaction (dPCR) [112], insulated Isothermal PCR (iiPCR) [113], offering promising prospects for detection of viral aerosols. As for air sampling devices, Li et al. used two different air samplers with different flow rates to collect aerosols within and between barns respectively, demonstrating the aerosol transmission of ASFV under field conditions [78]. In a separate study, Lee et al. developed a portable integrated bioaerosol sampling/ monitoring platform that can detect viral aerosol particles within 20 min using the signal of near-infrared (NIR)-to-NIR nanoprobe [114]. Moreover, Yao et al. have successfully developed an ultrasensitive and rapid “sample-to-answer” microsystem for on-site monitoring of SARS-CoV-2 in aerosols, which has been effectively implemented in various public settings including airports and hospitals [115]. The mobility, high sensitivity, and capability of these

aforementioned techniques to capture aerosols in open spaces align precisely with the needs of contemporary pig farms. The potential integration of such devices within pig farms would undoubtedly enhance the efficacy of viral aerosol detection.

Air pretreatment

The process of air pretreatment involves the elimination of pathogens from the air prior to its entry into the barn, with the aim of ensuring its safety. A viable approach entails the implementation of air filtration systems to purify the air entering pig barns, a strategy that has been extensively employed in global large-scale pig farms, demonstrating its efficacy in disease control, particularly in the case of PRRS [116, 117]. However, the cost and maintenance requirements of air filtration systems make them affordable only for large-scale farming enterprises. An alternative, more cost-effective method is air disinfection. Previous studies have demonstrated the efficacy of chlorine dioxide aerosol as a disinfectant in fitness centers [118], and it has also shown promising results in the disinfection of ASFV, IAV, and *Mycobacterium* [119, 120]. Hence, the utilization of chlorine dioxide as a means of air pre-treatment in pig barns exhibits considerable promise. Furthermore, the exploration of chlorine dioxide's potential as a sustained-release formulation for ongoing disinfection within the barn presents a viable option. Additionally, studies have indicated that ions produced by electrostatic disinfectors and ozone gas demonstrate efficacy in disinfecting and managing airborne aerosols containing SARS-CoV-2 [121, 122], thereby suggesting their potential applicability in pig farming settings.

Others

Other methods, such as the reduction of dust levels in pig barns and the establishment of disease-free zones, hold potential for the prevention and control of viral aerosols [2, 8]. Additionally, nasal vaccination, which can elicit both humoral and cellular immune responses, offers effective protection against respiratory pathogens, as the nasal cavity serves as the primary entry route for airborne pathogens [123]. Consequently, nasal vaccination presents a promising approach for attaining optimal protection against respiratory pathogens.

Conclusion

In conclusion, this review provides a systematic classification and summary of prevalent airborne-transmitted viruses in pig production. As shown in Fig. 1, it encompasses the transmission characteristics, influential factors, and preventive strategies, with the objective of offering valuable references and innovative perspectives

for mitigating and managing aerosol transmission. The significance of early-warning systems for viral aerosols, the enhancement of detection sensitivity and air sampler collection efficiency, as well as the development of air pretreatment strategies, are emphasized as crucial measures to establish a low-risk environment with fresh air for pig herds in the future.

Abbreviations

FMDV	Foot-and-mouth disease virus
PRRSV	Porcine reproductive and respiratory syndrome virus
IAV	Influenza A viruses
PEDV	Porcine epidemic diarrhea virus
PRV	Pseudorabies virus
CSFV	Classical swine fever virus
ASFV	African swine fever virus
PCV	Porcine circovirus
SVDV	Swine vesicular disease virus
JEV	Japanese encephalitis virus
PRCV	Porcine respiratory coronavirus
MHYO	<i>Mycoplasma hyopneumoniae</i>
RH	Relative humidity
dPCR	Digital polymerase chain reaction
iiPCR	Insulated isothermal PCR
NIR	Near-infrared

Acknowledgements

Not applicable.

Author contributions

XL, ZH and CJ conceived and designed structure of this paper. ZH, XT, RL and CJ collected information. ZH and XT wrote the original draft. XL reviewed and edited the manuscript. All authors read and approved the final manuscript.

Funding

This work was supported by Taishan Industry Leadership Talent Project of Shandong province in China, and the earmarked fund for CARS (CARS-35) and National Key R&D Program of China (2021ZD0113800).

Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 28 July 2023 Accepted: 25 October 2023

Published online: 31 October 2023

References

- Kedkovid R, Sirisereewan C, Thanawongnuwech R. Major swine viral diseases: an Asian perspective after the African swine fever introduction. *Porcine Health Manag.* 2020;6:20.
- Alarcón LV, Allepuz A, Mateu E. Biosecurity in pig farms: a review. *Porcine Health Manag.* 2021;7(1):5.

3. StÅrk KDC. The role of infectious aerosols in disease transmission in pigs. *Vet J.* 1999;158(3):164–81.
4. Jones RM, Brosseau LM. Aerosol transmission of infectious disease. *J Occup Environ Med.* 2015;57(5):501–8.
5. Chao CYH, Wan MP, Morawska L, Johnson GR, Ristovski ZD, Hargreaves M, Mengersen K, Corbett S, Li Y, Xie X, et al. Characterization of expiration air jets and droplet size distributions immediately at the mouth opening. *J Aerosol Sci.* 2009;40(2):122–33.
6. Jones AM, Harrison RM. The effects of meteorological factors on atmospheric bioaerosol concentrations—a review. *Sci Total Environ.* 2004;326(1–3):151–80.
7. Schlesinger RB, Cassee F. Atmospheric secondary inorganic particulate matter: the toxicological perspective as a basis for health effects risk assessment. *Inhal Toxicol.* 2003;15(3):197–235.
8. Stark KD. The role of infectious aerosols in disease transmission in pigs. *Vet J.* 1999;158(3):164–81.
9. Duchaine C, Roy CJ. Bioaerosols and airborne transmission: integrating biological complexity into our perspective. *Sci Total Environ.* 2022;825:154117.
10. Wang CC, Prather KA, Sznitman J, Jimenez JL, Lakdawala SS, Tufekci Z, Marr LC. Airborne transmission of respiratory viruses. *Science.* 2021;373:6558.
11. Roy CJ, Milton DK. Airborne transmission of communicable infection—the elusive pathway. *N Engl J Med.* 2004;350(17):1710–2.
12. Bischoff W, Russell G, Willard E, Stehle J Jr. Impact of a novel mobile high-efficiency particulate air-ultraviolet air recirculation system on the bacterial air burden during routine care. *Am J Infect Control.* 2019;47(8):1025–7.
13. Belsham GJ. Distinctive features of foot-and-mouth disease virus, a member of the picornavirus family; aspects of virus protein synthesis, protein processing and structure. *Prog Biophys Mol Biol.* 1993;60(3):241–60.
14. Donaldson AI, Gloster J, Harvey LD, Deans DH. Use of prediction models to forecast and analyse airborne spread during the foot-and-mouth disease outbreaks in Brittany, Jersey and the Isle of Wight in 1981. *Vet Rec.* 1982;110(3):53–7.
15. Sørensen JH, Mackay DK, Jensen CO, Donaldson AI. An integrated model to predict the atmospheric spread of foot-and-mouth disease virus. *Epidemiol Infect.* 2000;124(3):577–90.
16. Sørensen JH, Jensen CØ, Mikkelsen T, Mackay DKJ, Donaldson AI. Modelling the atmospheric dispersion of foot-and-mouth disease virus for emergency preparedness. *Phys Chem Earth Part B.* 2001;26(2):93–7.
17. Hugh-Jones ME, Wright PB. Studies on the 1967–8 foot-and-mouth disease epidemic. The relation of weather to the spread of disease. *J Hyg (Lond).* 1970;68(2):253–71.
18. Donaldson AI, Alexandersen S. Predicting the spread of foot and mouth disease by airborne virus. *Rev Sci Tech.* 2002;21(3):569–75.
19. Gloster J, Sellers RF, Donaldson AI. Long distance transport of foot-and-mouth disease virus over the sea. *Vet Rec.* 1982;110(3):47–52.
20. Kitching RP, Hutber AM, Thrusfield MV. A review of foot-and-mouth disease with special consideration for the clinical and epidemiological factors relevant to predictive modelling of the disease. *Vet J.* 2005;169(2):197–209.
21. Alexandersen S, Brotherhood I, Donaldson AI. Natural aerosol transmission of foot-and-mouth disease virus to pigs: minimal infectious dose for strain O1 Lausanne. *Epidemiol Infect.* 2002;128(2):301–12.
22. Pacheco JM, Tucker M, Hartwig E, Bishop E, Arzt J, Rodriguez LL. Direct contact transmission of three different foot-and-mouth disease virus strains in swine demonstrates important strain-specific differences. *Vet J.* 2012;193(2):456–63.
23. Sellers RF, Parker J. Airborne excretion of foot-and-mouth disease virus. *J Hyg (Lond).* 1969;67(4):671–7.
24. Alexandersen S, Donaldson AI. Further studies to quantify the dose of natural aerosols of foot-and-mouth disease virus for pigs. *Epidemiol Infect.* 2002;128(2):313–23.
25. Eble P, de Koeijer A, Bouma A, Stegeman A, Dekker A. Quantification of within- and between-pen transmission of foot-and-mouth disease virus in pigs. *Vet Res.* 2006;37(5):647–54.
26. Bartley LM, Donnelly CA, Anderson RM. Review of foot-and-mouth disease virus survival in animal excretions and on fomites. *Vet Rec.* 2002;151(22):667–9.
27. Veit M, Matczuk AK, Sinhadri BC, Krause E, Thaa B. Membrane proteins of arterivirus particles: structure, topology, processing and function. *Virus Res.* 2014;194:16–36.
28. Kristensen CS, Botner A, Takai H, Nielsen JP, Jorsal SE. Experimental airborne transmission of PRRS virus. *Vet Microbiol.* 2004;99(3–4):197–202.
29. Dee SA, Deen J, Jacobson L, Rossow KD, Mahlum C, Pijoan C. Laboratory model to evaluate the role of aerosols in the transport of porcine reproductive and respiratory syndrome virus. *Vet Rec.* 2005;156(16):501–4.
30. Otake S, Dee S, Corzo C, Oliveira S, Deen J. Long-distance airborne transport of infectious PRRSV and *Mycoplasma hyopneumoniae* from a swine population infected with multiple viral variants. *Vet Microbiol.* 2010;145(3–4):198–208.
31. Torremorell M, Pijoan C, Janni K, Walker R, Joo HS. Airborne transmission of *Actinobacillus pleuropneumoniae* and porcine reproductive and respiratory syndrome virus in nursery pigs. *Am J Vet Res.* 1997;58(8):828–32.
32. Cho JG, Deen J, Dee SA. Influence of isolate pathogenicity on the aerosol transmission of Porcine reproductive and respiratory syndrome virus. *Can J Vet Res.* 2007;71(1):23–7.
33. Cho JG, Dee SA, Deen J, Trincado C, Fano E, Jiang Y, Faaberg K, Murtaugh MP, Guedes A, Collins JE, et al. The impact of animal age, bacterial coinfection, and isolate pathogenicity on the shedding of porcine reproductive and respiratory syndrome virus in aerosols from experimentally infected pigs. *Can J Vet Res.* 2006;70(4):297–301.
34. Brockmeier SL, Palmer MV, Bolin SR. Effects of intranasal inoculation of porcine reproductive and respiratory syndrome virus, *Bordetella bronchiseptica*, or a combination of both organisms in pigs. *Am J Vet Res.* 2000;61(8):892–9.
35. Alonso C, Raynor PC, Davies PR, Torremorell M. Concentration, size distribution, and infectivity of airborne particles carrying swine viruses. *PLoS ONE.* 2015;10(8):e0135675.
36. Hermann J, Hoff S, Munoz-Zanzi C, Yoon KJ, Roof M, Burkhardt A, Zimmerman J. Effect of temperature and relative humidity on the stability of infectious porcine reproductive and respiratory syndrome virus in aerosols. *Vet Res.* 2007;38(1):81–93.
37. Huang QJ, Song K, Xu C, Bolon DNA, Wang JP, Finberg RW, Schiffer CA, Somasundaran M. Quantitative structural analysis of influenza virus by cryo-electron tomography and convolutional neural networks. *Structure.* 2022;30(5):777–86e3.
38. Prost K, Kloeze H, Mukhi S, Bozek K, Poljak Z, Mubareka S. Bioaerosol and surface sampling for the surveillance of influenza A virus in swine. *Transbound Emerg Dis.* 2019;66(3):1210–7.
39. Neira V, Rabinowitz P, Rendahl A, Paccha B, Gibbs SG, Torremorell M. Characterization of viral load, viability and persistence of influenza A virus in air and on surfaces of swine production facilities. *PLoS ONE.* 2016;11(1):e0146616.
40. Corzo CA, Culhane M, Dee S, Morrison RB, Torremorell M. Airborne detection and quantification of swine influenza A virus in air samples collected inside, outside and downwind from swine barns. *PLoS ONE.* 2013;8(8):e71444.
41. Zhang H, Li X, Ma R, Li X, Zhou Y, Dong H, Li X, Li Q, Zhang M, Liu Z, et al. Airborne spread and infection of a novel swine-origin influenza A (H1N1) virus. *Virology.* 2013;10:204.
42. Mubareka S, Lowen AC, Steel J, Coates AL, García-Sastre A, Palese P. Transmission of influenza virus via aerosols and fomites in the guinea pig model. *J Infect Dis.* 2009;199(6):858–65.
43. Herfst S, Schrauwen EJ, Linster M, Chutinimitkul S, de Wit E, Munster VJ, Sorrell EM, Bestebroer TM, Burke DF, Smith DJ, et al. Airborne transmission of influenza A/H5N1 virus between ferrets. *Science.* 2012;336(6088):1534–41.
44. Lv J, Wei L, Yang Y, Wang B, Liang W, Gao Y, Xia X, Gao L, Cai Y, Hou P, et al. Amino acid substitutions in the neuraminidase protein of an H9N2 avian influenza virus affect its airborne transmission in chickens. *Vet Res.* 2015;46(1):44.
45. Zhang W, Shi Y, Lu X, Shu Y, Qi J, Gao GF. An airborne transmissible avian influenza H5 hemagglutinin seen at the atomic level. *Science.* 2013;340(6139):1463–7.
46. Weber TP, Stilianakis NI. Inactivation of influenza A viruses in the environment and modes of transmission: a critical review. *J Infect.* 2008;57(5):361–73.

47. Lowen AC, Mubareka S, Steel J, Palese P. Influenza virus transmission is dependent on relative humidity and temperature. *PLoS Pathog.* 2007;3(10):1470–6.
48. Lindsley WG, Blachere FM, Thewlis RE, Vishnu A, Davis KA, Cao G, Palmer JE, Clark KE, Fisher MA, Khakoo R, et al. Measurements of airborne influenza virus in aerosol particles from human coughs. *PLoS ONE.* 2010;5(11):e15100.
49. Pensaert MB, de Bouck P. A new coronavirus-like particle associated with diarrhea in swine. *Arch Virol.* 1978;58(3):243–7.
50. Sun J, Li Q, Shao C, Ma Y, He H, Jiang S, Zhou Y, Wu Y, Ba S, Shi L, et al. Isolation and characterization of Chinese porcine epidemic diarrhea virus with novel mutations and deletions in the S gene. *Vet Microbiol.* 2018;221:81–9.
51. Alonso C, Goede DP, Morrison RB, Davies PR, Rovira A, Marthaler DG, Torremorell M. Evidence of infectivity of airborne porcine epidemic diarrhea virus and detection of airborne viral RNA at long distances from infected herds. *Vet Res.* 2014;45(1):73.
52. Jung K, Saif LJ, Wang Q. Porcine epidemic diarrhea virus (PEDV): an update on etiology, transmission, pathogenesis, and prevention and control. *Virus Res.* 2020;286:198045.
53. Tun HM, Cai Z, Khafipour E. Monitoring survivability and infectivity of porcine epidemic Diarrhea virus (PEDV) in the infected on-farm earthen manure storages (EMS). *Front Microbiol.* 2016;7:265.
54. Gallien S, Andraud M, Moro A, Lediguerher G, Morin N, Gauger PC, Bigault L, Paboouf F, Berri M, Rose N, et al. Better horizontal transmission of a US non-InDel strain compared with a French InDel strain of porcine epidemic diarrhoea virus. *Transbound Emerg Dis.* 2018;65(6):1720–32.
55. Beam A, Goede D, Fox A, McCool MJ, Wall G, Haley C, Morrison R. A porcine epidemic Diarrhea virus outbreak in one geographic region of the United States: descriptive epidemiology and investigation of the possibility of airborne virus spread. *PLoS ONE.* 2015;10(12):e0144818.
56. Li Y, Wu Q, Huang L, Yuan C, Wang J, Yang Q. An alternative pathway of enteric PEDV dissemination from nasal cavity to intestinal mucosa in swine. *Nat Commun.* 2018;9(1):3811.
57. Niederwerder MC, Nietfeld JC, Bai J, Peddireddi L, Breazeale B, Anderson J, Kerrigan MA, An B, Oberst RD, Crawford K, et al. Tissue localization, shedding, virus carriage, antibody response, and aerosol transmission of Porcine epidemic diarrhea virus following inoculation of 4-week-old feeder pigs. *J Vet Diagn Invest.* 2016;28(6):671–8.
58. Zheng HH, Fu PF, Chen HY, Wang ZY. Pseudorabies virus: from pathogenesis to prevention strategies. *Viruses.* 2022;14(8):1638.
59. Donaldson AI, Wardley RC, Martin S, Ferris NP. Experimental Aujeszky's disease in pigs: excretion, survival and transmission of the virus. *Vet Rec.* 1983;113(21):490–4.
60. Grant RH, Scheidt AB, Rueff LR. Aerosol transmission of a viable virus affecting swine: explanation of an epizootic of pseudorabies. *Int J Biometeorol.* 1994;38(1):33–9.
61. Christensen LS, Mousing J, Mortensen S, Soerensen KJ, Strandbygaard SB, Henriksen CA, Andersen JB. Evidence of long distance airborne transmission of Aujeszky's disease (pseudorabies) virus. *Vet Rec.* 1990;127(19):471–4.
62. Christensen LS, Mortensen S, Botner A, Strandbygaard BS, Ronsholt L, Henriksen CA, Andersen JB. Further evidence of long distance airborne transmission of Aujeszky's disease (pseudorabies) virus. *Vet Rec.* 1993;132(13):317–21.
63. Wang Z, Min G, Li M, Teng J, Ding M. Study on the morphological processing of classical swine fever virus in cultured cells. *Wei Sheng Wu Xue Bao.* 2000;40(3):237–42.
64. Elbers AR, Stegeman JA, de Jong MC. Factors associated with the introduction of classical swine fever virus into pig herds in the central area of the 1997/98 epidemic in The Netherlands. *Vet Rec.* 2001;149(13):377–82.
65. Gonzalez C, Pijoan C, Ciprian A, Correa P, Mendoza S. The effect of vaccination with the PAV-250 strain classical swine fever (CSF) virus on the airborne transmission of CSF virus. *J Vet Med Sci.* 2001;63(9):991–6.
66. Lu X, Ward MP. Spatiotemporal analysis of reported classical swine fever outbreaks in China (2005–2018) and the influence of weather. *Transbound Emerg Dis.* 2022;69(5):e3183–95.
67. Laevens H, Koenen F, Deluyker H, Berkvens D, de Kruijf A. An experimental infection with classical swine fever virus in weaner pigs. I. Transmission of the virus, course of the disease, and antibody response. *Vet Q.* 1998;20(2):41–5.
68. Laevens H, Koenen F, Deluyker H, de Kruijf A. Experimental infection of slaughter pigs with classical swine fever virus: transmission of the virus, course of the disease and antibody response. *Vet Rec.* 1999;145(9):243–8.
69. Weesendorp E, Backer J, Loeffen W. Quantification of different classical swine fever virus transmission routes within a single compartment. *Vet Microbiol.* 2014;174(3–4):353–61.
70. Weesendorp E, Stegeman A, Loeffen WL. Quantification of classical swine fever virus in aerosols originating from pigs infected with strains of high, moderate or low virulence. *Vet Microbiol.* 2009;135(3–4):222–30.
71. Weesendorp E, Landman WJ, Stegeman A, Loeffen WL. Detection and quantification of classical swine fever virus in air samples originating from infected pigs and experimentally produced aerosols. *Vet Microbiol.* 2008;127(1–2):50–62.
72. Andres G, Simon-Mateo C, Vinuela E. Assembly of African swine fever virus: role of polyprotein pp220. *J Virol.* 1997;71(3):2331–41.
73. Xue Q, Liu H, Zhu Z, Yang F, Song Y, Li Z, Xue Z, Cao W, Liu X, Zheng H. African swine fever virus regulates host energy and amino acid metabolism to promote viral replication. *J Virol.* 2022;96(4):e0191921.
74. Sánchez-Vizcaino JM, Mur L, Gomez-Villamandos JC, Carrasco L. An update on the epidemiology and pathology of African swine fever. *J Comp Pathol.* 2015;152(1):9–21.
75. Penrith ML, Vosloo W. Review of African swine fever: transmission, spread and control. *J S Afr Vet Assoc.* 2009;80(2):58–62.
76. Wilkinson PJ, Donaldson AI. Transmission studies with African swine fever virus. The early distribution of virus in pigs infected by airborne virus. *J Comp Pathol.* 1977;87(3):497–501.
77. Olesen AS, Lohse L, Boklund A, Halasa T, Gallardo C, Pejsak Z, Belsham GJ, Rasmussen TB, Botner A. Transmission of African swine fever virus from infected pigs by direct contact and aerosol routes. *Vet Microbiol.* 2017;211:92–102.
78. Li X, Hu Z, Fan M, Tian X, Wu W, Gao W, Bian L, Jiang X. Evidence of aerosol transmission of African swine fever virus between two piggeries under field conditions: a case study. *Front Vet Sci.* 2023;10:1201503.
79. Liu Y, Zhang X, Qi W, Yang Y, Liu Z, An T, Wu X, Chen J. Prevention and control strategies of African swine fever and progress on pig farm repopulation in China. *Viruses.* 2021;13(12):2552.
80. Pietschmann J, Guinat C, Beer M, Pronin V, Tauscher K, Petrov A, Keil G, Blome S. Course and transmission characteristics of oral low-dose infection of domestic pigs and European wild boar with a Caucasian African swine fever virus isolate. *Arch Virol.* 2015;160(7):1657–67.
81. de Carvalho Ferreira HC, Weesendorp E, Quak S, Stegeman JA, Loeffen WL. Quantification of airborne African swine fever virus after experimental infection. *Vet Microbiol.* 2013;165(3–4):243–51.
82. Allan GM, McNeilly F, Kennedy S, Daft B, Clarke EG, Ellis JA, Haines DM, Meehan BM, Adair BM. Isolation of porcine circovirus-like viruses from pigs with a wasting disease in the USA and Europe. *J Vet Diagn Invest.* 1998;10(1):3–10.
83. Segalés J. Porcine circovirus type 2 (PCV2) infections: clinical signs, pathology and laboratory diagnosis. *Virus Res.* 2012;164(1–2):10–9.
84. Verreault D, Letourneau V, Gendron L, Masse D, Gagnon CA, Duchaine C. Airborne porcine circovirus in Canadian swine confinement buildings. *Vet Microbiol.* 2010;141(3–4):224–30.
85. Zhai SL, Lu SS, Wei WK, Lv DH, Wen XH, Zhai Q, Chen QL, Sun YW, Xi Y. Reservoirs of porcine circoviruses: a mini review. *Front Vet Sci.* 2019;6:319.
86. Borkenhagen LK, Mallinson KA, Tsao RW, Ha SJ, Lim WH, Toh TH, Anderson BD, Fieldhouse JK, Philo SE, Chong KS, et al. Surveillance for respiratory and diarrheal pathogens at the human-pig interface in Sarawak, Malaysia. *PLoS ONE.* 2018;13(7):e0201295.
87. Lin F, Kitching RP. Swine vesicular disease: an overview. *Vet J.* 2000;160(3):192–201.
88. Liebermann H, Schulze P, Riebe R, Koitzsch R. Physico-chemical properties of swine vesicular disease virus. *Arch Exp Veterinarmed.* 1976;30(3):433–40.
89. Sellers RF, Herniman KA. The airborne excretion by pigs of swine vesicular disease virus. *J Hyg (Lond).* 1974;72(1):61–5.

90. Dekker A, Moonen P, de Boer-Luijtz EA, Terpstra C. Pathogenesis of swine vesicular disease after exposure of pigs to an infected environment. *Vet Microbiol.* 1995;45(2–3):243–50.
91. Sellers RF, Herniman KA. The effects of spraying on the amounts of airborne foot-and-mouth disease virus present in loose-boxes. *J Hyg (Lond).* 1972;70(3):551–6.
92. Okuno Y, Igarashi A, Fukunaga T, Tadano M, Fukai K. Electron microscopic observation of a newly isolated flavivirus-like virus from field-caught mosquitoes. *J Gen Virol.* 1984;65(Pt 4):803–7.
93. Garcia-Nicolas O, Braun RO, Milona P, Lewandowska M, Dijkman R, Alves MP, Summerfield A. Targeting of the nasal mucosa by Japanese encephalitis virus for non-vector-borne transmission. *J Virol.* 2018;92:24.
94. Lyons AC, Huang YS, Park SL, Ayers VB, Hettenbach SM, Higgs S, McVey DS, Noronha L, Hsu WW, Vanlandingham DL. Shedding of Japanese encephalitis virus in oral fluid of infected swine. *Vector Borne Zoonotic Dis.* 2018;18(9):469–74.
95. Park SL, Huang YS, Lyons AC, Ayers VB, Hettenbach SM, McVey DS, Burton KR, Higgs S, Vanlandingham DL. North American domestic pigs are susceptible to experimental infection with Japanese encephalitis virus. *Sci Rep.* 2018;8(1):7951.
96. Ricklin ME, Garcia-Nicolas O, Brechbuhl D, Python S, Zumkehr B, Nougairede A, Charrel RN, Posthaus H, Oevermann A, Summerfield A. Vector-free transmission and persistence of Japanese encephalitis virus in pigs. *Nat Commun.* 2016;7:10832.
97. Chai C, Palinski R, Xu Y, Wang Q, Cao S, Geng Y, Zhao Q, Wen Y, Huang X, Yan Q, et al. Aerosol and contact transmission following intranasal infection of mice with Japanese encephalitis virus. *Viruses.* 2019;11(1):87.
98. Turliewicz-Podbielska H, Pomorska-Mol M. Porcine coronaviruses: overview of the state of the art. *Virol Sin.* 2021;36(5):833–51.
99. Cantero M, Carlero D, Chichon FJ, Martin-Benito J, De Pablo PJ. Monitoring SARS-CoV-2 surrogate TGEV individual virions structure survival under harsh physicochemical environments. *Cells.* 2022;11(11):1759.
100. Laude H, Van Reeth K, Pensaert M. Porcine respiratory coronavirus: molecular features and virus-host interactions. *Vet Res.* 1993;24(2):125–50.
101. Jung K, Alekseev KP, Zhang X, Cheon DS, Vlasova AN, Saif LJ. Altered pathogenesis of porcine respiratory coronavirus in pigs due to immunosuppressive effects of dexamethasone: implications for corticosteroid use in treatment of severe acute respiratory syndrome coronavirus. *J Virol.* 2007;81(24):13681–93.
102. Van Reeth K, Labarque G, Nauwynck H, Pensaert M. Differential production of proinflammatory cytokines in the pig lung during different respiratory virus infections: correlations with pathogenicity. *Res Vet Sci.* 1999;67(1):47–52.
103. Costantini V, Lewis P, Alsop J, Templeton C, Saif LJ. Respiratory and fecal shedding of porcine respiratory coronavirus (PRCV) in sentinel weaned pigs and sequence of the partial S-gene of the PRCV isolates. *Arch Virol.* 2004;149(5):957–74.
104. Bourgueil E, Hutet E, Cariolet R, Vannier P. Experimental infection of pigs with the porcine respiratory coronavirus (PRCV): measure of viral excretion. *Vet Microbiol.* 1992;31(1):11–8.
105. Cox E, Hooyberghs J, Pensaert MB. Sites of replication of a porcine respiratory coronavirus related to transmissible gastroenteritis virus. *Res Vet Sci.* 1990;48(2):165–9.
106. Keep S, Carr BV, Lean FZX, Fones A, Newman J, Dowgier G, Freimanis G, Vatzia E, Polo N, Everest H, et al. Porcine respiratory coronavirus as a model for acute respiratory coronavirus disease. *Front Immunol.* 2022;13: 867707.
107. Cox CS. Airborne bacteria and viruses. *Sci Prog.* 1989;73(292 Pt 4):469–99.
108. Zhang Z, Li X, Lyu K, Zhao X, Zhang F, Liu D, Zhao Y, Gao F, Hu J, Xu D. Exploring the transmission path, influencing factors and risk of aerosol transmission of SARS-CoV-2 at Xi'an Xianyang International Airport. *Int J Environ Res Public Health.* 2023;20(1):865.
109. Brownstein JS, Holford TR, Fish D. Enhancing West Nile virus surveillance. *U S Emerg Infect Dis.* 2004;10(6):1129–33.
110. Silva RR, Ribeiro CJN, Moura TR, Santos MB, Santos AD, Tavares DS, Santos PL. Basic sanitation: a new indicator for the spread of COVID-19? *Trans R Soc Trop Med Hyg.* 2021;115(7):832–40.
111. Anderson BD, Lednický JA, Torremorell M, Gray GC. The use of bio-aerosol sampling for airborne virus surveillance in swine production facilities: a mini review. *Front Vet Sci.* 2017;4:121.
112. Wu X, Xiao L, Lin H, Chen S, Yang M, An W, Wang Y, Yang Z, Yao X, Tang Z. Development and application of a droplet digital polymerase chain reaction (ddPCR) for detection and investigation of African swine fever virus. *Can J Vet Res.* 2018;82(1):70–4.
113. Zou T, Deng J, Li X, Zhang S, Chen L, Hao L, Zhuang J, Wang H, Zhang G, Ge S, et al. Development of a fluorescent probe hydrolysis-insulated isothermal PCR for rapid and sensitive on-site detection of African swine fever virus. *Virol Sin.* 2022;37(3):462–4.
114. Lee I, Seok Y, Jung H, Yang B, Lee J, Kim J, Pyo H, Song CS, Choi W, Kim MG, et al. Integrated bioaerosol sampling/monitoring platform: field-deployable and rapid detection of airborne viruses. *ACS Sens.* 2020;5(12):3915–22.
115. Li S, Li B, Li X, Liu C, Qi X, Gu Y, Lin B, Sun L, Chen L, Han B, et al. An ultrasensitive and rapid “sample-to-answer” microsystem for on-site monitoring of SARS-CoV-2 in aerosols using “in situ” tetra-primer recombinase polymerase amplification. *Biosens Bioelectron.* 2023;219: 114816.
116. Alonso C, Murtaugh MP, Dee SA, Davies PR. Epidemiological study of air filtration systems for preventing PRRSV infection in large sow herds. *Prev Vet Med.* 2013;112(1–2):109–17.
117. Alonso C, Davies PR, Polson DD, Dee SA, Lazarus WF. Financial implications of installing air filtration systems to prevent PRRSV infection in large sow herds. *Prev Vet Med.* 2013;111(3–4):268–77.
118. Boonrattanakij N, Yomchinda S, Lin FJ, Bellotindos LM, Lu MC. Investigation and disinfection of bacteria and fungi in sports fitness center. *Environ Sci Pollut Res Int.* 2021;28(37):52576–86.
119. Jefri U, Khan A, Lim YC, Lee KS, Liew KB, Kassab YW, Choo CY, Al-Worafi YM, Ming LC, Kalusalingam A. A systematic review on chlorine dioxide as a disinfectant. *J Med Life.* 2022;15(3):313–8.
120. Wei R, Wang X, Cao Y, Gong L, Liu X, Zhang G, Guo C. Chlorine dioxide inhibits African swine fever virus by blocking viral attachment and destroying viral nucleic acids and proteins. *Front Vet Sci.* 2022;9: 844058.
121. Feng Z, Cao SJ, Wang J, Kumar P, Haghghat F. Indoor airborne disinfection with electrostatic disinfectant (ESD): numerical simulations of ESD performance and reduction of computing time. *Build Environ.* 2021;200: 107956.
122. Cao J, Zhang Y, Chen Q, Yao M, Pei R, Wang Y, Yue Y, Huang Y, Wang J, Guan W. Ozone gas inhibits SARS-CoV-2 transmission and provides possible control measures. *Aerosol Sci Eng.* 2021;5(4):516–23.
123. Neutra MR, Kozłowski PA. Mucosal vaccines: the promise and the challenge. *Nat Rev Immunol.* 2006;6(2):148–58.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

