

Original Contribution

Large-Scale Serological Survey of Influenza A Virus in South Korean Wild Boar (*Sus scrofa*)

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Abstract: In this comprehensive large-scale study, conducted from 2015 to 2019, 7,209 wild boars across South Korea were sampled to assess their exposure to influenza A viruses (IAVs). Of these, 250 (3.5%) were found to be IAV-positive by ELISA, and 150 (2.1%) by the hemagglutination inhibition test. Detected subtypes included 23 cases of pandemic 2009 H1N1, six of human seasonal H3N2, three of classical swine H1N1, 13 of triple-reassortant swine H1N2, seven of triple-reassortant swine H3N2, and seven of swine-origin H3N2 variant. Notably, none of the serum samples tested positive for avian IAV subtypes H3N8, H5N3, H7N7, and H9N2 or canine IAV subtype H3N2. This serologic analysis confirmed the exposure of Korean wild boars to various subtypes of swine and human influenza viruses, with some serum samples cross-reacting between swine and human strains, indicating potential infections with multiple IAVs. The results highlight the potential of wild boar as a novel mixing vessel, facilitating the adaptation of IAVs and their spillover to other hosts, including humans. In light of these findings, we recommend regular and frequent surveillance of circulating influenza viruses in the wild boar population as a proactive measure to prevent potential human influenza pandemics and wild boar influenza epizootics.

Keywords: Serology, Influenza A viruses, Korean wild boars, Swine viruses, Spillover, Pandemic H1N1, IAV surveillance, Wild boar infection, Human-swine virus transmission

INTRODUCTION

Influenza viruses are segmented RNA viruses belonging to the family Orthomyxoviridae, which includes three different influenza virus genera (A, B, and C) (Foni et al., 2013; Kovalenko et al., 2017). Influenza viruses are classified into

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10393-024-01685-8>.

Published online: June 6, 2024

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various subtypes by the surface glycoproteins hemagglutinin (HA) and neuraminidase (NA). To date, 16 HA and 9 NA type A influenza virus subtypes have been identified (Siembieda et al., 2011). The major reservoirs of influenza viruses are wild waterbirds of the orders Anseriformes and Charadriiformes; however, they can infect humans and other species, including swine, avian, feline, canine, equine, minks, sea mammals, ferrets, and bats (Martin et al., 2017; Hemert et al., 2019). Among these, swine are an important source of influenza viruses. With common cellular receptors with birds and humans, swine provide opportunities for mixed infections and the possibility of genetic reassortment among avian, human, and swine influenza viruses (Hall et al., 2008). Thus, swine are considered to be "mixing vessels" or intermediate hosts for influenza viruses, and new influenza virus can emerge through the genetic reassortment of existing strains. The impact of influenza epidemics has been significant, particularly the 2009 H1N1 pandemic influenza virus (H1N1pdm09) that caused a worldwide pandemic in 2009. The total number of deaths during this period is estimated to be 151,700–575,400 (Clayton et al., 2022). Because H1N1pdm09 has been repeatedly transmitted from humans to swine, reassortment between swine and the H1N1pdm09 virus has been reported in many countries (Rajão et al., 2017), resulting in the generation of new strains of swine-origin influenza viruses such as the swine-origin H3N2 variant (sH3N2v) reassortment strain with swine H3N2 and H1N1pdm09 in swine. This virus has caused 430 infections in the US since 2010. In addition, the sH3N2v virus has been reported in several other countries, including Australia, Canada, China, and Vietnam (Anderson et al., 2021), providing strong evidence that swine influenza virus (SIV) circulating in swine herds poses a threat to public health and may cause another epidemic in the future.

Unlike domestic swine, wild boar is free-ranging and are therefore exposed to IAVs through contact with migratory waterfowl—a natural reservoir for IAVs—and animals from different habitats. Wild boar is one of the most widely distributed mammals in the world; not only can they migrate up to 150 km (Massei and Genov, 2004), but they also live in the same habitats as waterfowl, feed in the same agricultural areas, roll and swim in the same water bodies, and also prey on them (Hall et al., 2008). This high mobility and ability to adapt to various habitats increase opportunities for contact with domestic swine and humans.

Wild boars exhibit viral shedding patterns and antibody response dynamics similar to domestic swine, resulting in high infectivity and transmissibility (Sun et al., 2015). Furthermore, wild boars are susceptible to H3 and H6 avian IAVs, and viral shedding can occur for up to 6 days (Martin et al., 2017). The 8-year lifespan of wild boars provides ample opportunity for reinfection and recombination of more antigenically distinct IAVs. Thus, wild boars are a dynamic mixing vessel for IAVs (Feng et al., 2014).

As a source of infectious diseases, wild boars pose risks to both livestock and humans. Hepatitis E virus (HEV) has been documented as direct evidence of transmission from wild boar to humans. Classical swine fever virus (CSFV), pseudorabies virus (PRV), African swine fever virus (ASFV), porcine circovirus type 2 (PCV2), porcine reproductive and respiratory syndrome virus (PRRSV), and porcine parvovirus (PPV) can infect domestic swine and wild boar (Meng et al., 2009). Although no cases of influenza virus transmission from wild boar to humans have been reported, the risk of influenza A virus transmission from wild boar to humans is considered high due to the frequent sharing of certain subtypes, such as human-like H3N2 strains (Ruiz-Fons, 2017).

Wild boars have the potential to transmit influenza viruses to humans, but this area of research has not received much attention (Kovalenko et al., 2017). In this study, we examined the transmission of influenza viruses from different hosts and subtypes, including avian, human, canine, and swine influenza viruses.

MATERIALS AND METHODS

Sample Collection

From January 5, 2015, to September 27, 2019, the Korean Department of Agriculture, Livestock, and Quarantine collected postmortem serum samples from 7209 wild boars. This collection period included 2015 (1299 samples), 2016 (1504 samples), 2017 (1559 samples), 2018 (1230 samples), and 2019 (January 1 2019 to September 27 2019: 1617 samples). In addition, wild boars were captured from 13 regions: Seoul ($n=33$), Daegu ($n=46$), Gwangju ($n=52$), Daejeon ($n=1$), Gyeonggi ($n=942$), Gangwon ($n=1132$), Chungbuk ($n=765$), Chungnam ($n=951$), Jeonbuk ($n=317$), Jeonnam ($n=405$), Gyeongbuk ($n=1326$), Gyeongnam ($n=1170$), and Jeju ($n=54$). There were also samples ($n=15$) with uncertain regions.

Serologic Analyses

Antibody status was determined using VDPPro AIV Ab c-ELISA (Median Duo Sets; Median Diagnostics, Seoul, Korea). Serum samples with a sample-to-negative-control ratio of <0.5 were determined positive for IAV. Of the samples tested, 250 were identified as IAV-positive, and all of them were selected for subtyping by hemagglutination inhibition (HI) assay.

HI assays were performed according to the WHO manual (World Health Organization, 2011). Briefly, one volume of wild boar serum was treated with three volumes of a receptor-destroying enzyme (RDE; Denka Seiken Co., Tokyo, Japan) overnight at 37°C, followed by incubation at 56°C for 30 minutes to inactivate the RDE. The treated antisera were then diluted with six volumes of 1× phosphate-buffered saline. Then, 25 µL of serum was serially diluted twofold, mixed with 4 HA units of virus, incubated for 30 min at room temperature, and tested by reacting with 0.5% RBC for 30 minutes. The HI titer was defined as the reciprocal of the last serum dilution that completely inhibited hemagglutination. Serum samples were considered positive for a specific virus if the HI titers were $\geq 1:40$ and negative if they were $<1:40$ (Otani et al., 2022).

Viruses

A total of 11 influenza A viruses (IAVs) were selected for this study, representing a wide range of subtypes. These include:

1. A/Swine/Korea/GC0503/2005(H1N1), a classical swine IAV strain (sH1N1);
2. A/Swine/South Korea/6822/2006(H1N2), a triple-reassortant swine IAV strain (sH1N2);
3. A/Swine/Korea/GC0407/2005(H3N2), a triple-reassortant swine IAV strain (sH3N2);
4. A/Swine/South Korea/SNU2/2017(H3N2), a swine-origin variant IAV strain (sH3N2v);
5. A/California/04/2009(H1N1), a 2009 pandemic IAV strain (H1N1pdm09);
6. A/Philippines/2/1982(H3N2), a seasonal human IAV strain (hH3N2);
7. A/Canine/Korea/01/2007(H3N2), a canine IAV strain (cH3N2);
8. A/Wild Bird/South Korea/SNU3/2015(H7N7) (aH7N7);
9. A/Wild Bird/South Korea/SNU4/2015(H5N3) (aH5N3);

10. A/Wild Bird/South Korea/SNU5/2016(H3N8) (aH3N8);
11. A/Wild Bird/South Korea/SNU6/2018(H9N2) (aH9N2).

Each virus was propagated in specific-pathogen-free embryonated eggs. All swine, avian, and canine viruses, except for the human viruses, were isolated strains from Korea. The avian influenza viruses in this study belong to the low-pathogenic avian influenza (LPAI).

RESULTS

Of the 7209 wild boar serum samples that underwent seroprevalence analysis, 250 were classified as seropositive using ELISA. These 250 samples were tested using HI assays for the presence of antibodies to human H1N1pdm09, human H3N2, swine H1N1, swine H1N2, swine H3N2, swine H3N2v, avian H3N8, avian H5N3, avian H7N7, avian H9N2 and canine H3N2 influenza viruses. The remaining 100 specimens with an HI titer less than 40 for all strains were classified as an “indeterminate”. Fifty-nine of the 250 samples were unambiguously assigned to a subtype, and a further 91 were reactive to multiple antigens (Supplementary Tables 1).

A total of 113 human strain specimens were determined to be positive (23 specimens were positive for H1N1pdm09, six for human H3N2, and 87 for combined strains). In addition, 118 swine strain samples were positive (three for swine H1N1, 13 for swine H1N2, seven for swine H3N2, seven for swine H3N2v, and 88 for combined strains). However, no antibodies were detected against all avian strains or against canine H3N2. A higher percentage was found to be positive to more than two strains (1.26%, 91/7,209) than to only one strain (0.82%, 59/7,209). In addition, several combined reactivity patterns against two strains were found (0.76%, 55/7,209), and a few reactivities against more than three strains were also observed (0.50%, 36/7,209). See Supplementary Tables 1–2 for further details.

In terms of individually positive strains, H1N1pdm09 had the highest positive rate among all strains, with a positive rate of 1.18% (19/1,617) in 2019 and a total rate of 0.32% (23/7,209) for all years. In addition, human H3N2 was also positive and increased from 2015 to 2019. All swine strains had positive cases; among them, H1N2 infection was found to be consistently infectious each year. The number of positive cases for all virus strains increased

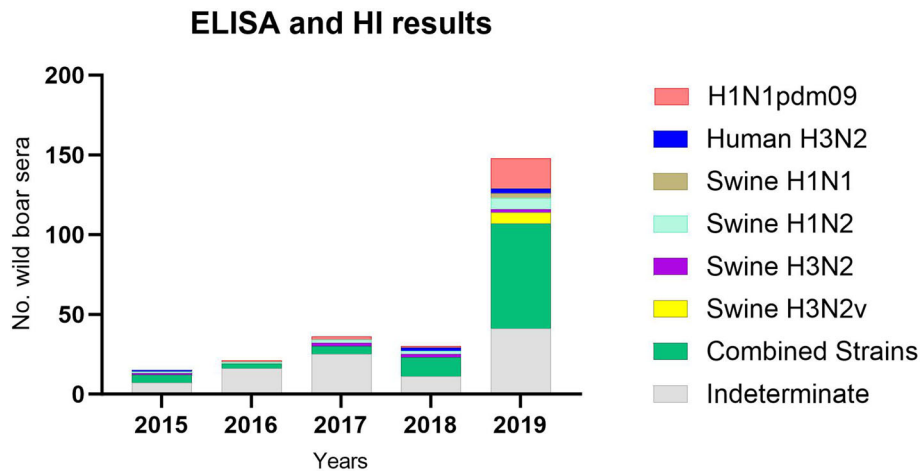


Figure 1. The number of positive samples in enzyme-linked immunosorbent assay (ELISA) and ratio of Hemagglutination Inhibition (HI) positive samples.

with each year. The percentage of ELISA-positive samples increased from 1.2% in 2015 to 9.2% in 2019. Combined infections had the highest infection rate in 2019. In addition, the distribution of the positive strains after HI testing showed that more diverse strains had caused infection, and the number of infections increased throughout 2019 (Fig. 1). However, the number of samples corresponding to unknown infections was significant. This number is expected to increase as other strains of the virus are tested.

From 2015 to 2019, all regions except Jeju showed positive results in all eight provinces (Fig. 2). In 2015 and 2016, the regions with the highest seropositivity rates determined through ELISA were Gyeongbuk (0.5% each). In 2017, Chungbuk had the highest rate of 1.0%, followed by Gyeongnam (0.7%) in 2018 and Gangwon in 2019, with the highest rate of 2.7% (Fig. 3).

DISCUSSION

This study aims to determine the prevalence of exposure to influenza A virus (IAV) and its specific subtypes in wild boar in South Korea. In particular, it focuses on identifying which specific IAV subtypes, especially those of human, canine and porcine origin, have been encountered by wild boar. This investigation explores the possibility that wild boars are simultaneously exposed to multiple IAV strains and act as dynamic 'mixing vessels' for the virus. To this end, the extent of exposure to various subtypes of influenza A virus in Korean wild boars was systematically investigated. This will contribute to the understanding of the role of wild boar in the influenza virus ecosystem.

In examining serological data from 2015 to 2019, we observe a noticeable increase in ELISA-positive samples among wild boar populations (Fig. 1). This upward trend in seroprevalence of wild boars from 2015 to 2019 may be due to the increase in population size and density of wild boars. According to a report from the National Institute of Biological Resources of Korea, the average population of wild boar in Korea has increased from 76,691 in 2015 to 84,795 in 2019 (with maximum of 160,397). In addition, the average density of wild boars in forested areas larger than 500m increased by 20% from 5.0 animals/km² in 2015 to 6.0 animals/km² in 2019 (Wild boar management I, 2019). This increased population density could facilitate the spread of disease, resulting in increased viral infections and transmissions. Furthermore, the age of wild boar may have influenced seroprevalence, as juvenile wild boars are more likely to spread disease within their group (Podgórski et al., 2018). However, the effect of the age structure of the wild boar population on the infection rate is difficult to determine with certainty, as the age of the animals was not confirmed in this study.

In this serological survey of the wild boar population in South Korea, a significant increase in the prevalence of the pandemic H1N1pdm09 strain was observed. Of the 7,209 wild boars sampled, 23 (0.32%) individuals were seropositive for the H1N1pdm09 strain. In addition, cross-reactivity with H1N1pdm09 and additional serotypes was observed in 87 (1.21%) individuals. Of particular note was the increased prevalence of this infection in the year 2019 (each). These findings suggest a potential for the geo-



Figure 2. Geographical distribution of wild boar in South Korea with positive serology by ELISA and HI for Influenza A viruses, 2015–2019. Graphic display was produced by using QGIS 3.12.3-Bucure-ti (<http://www.qgis.org>). Satellite image is from Kakaomap.

graphic spread of the H1N1pdm09 virus among wild boar populations.

Previous data from South Korea (2012) indicated that the prevalence of H1N1pdm09 in wild boar was higher than in other countries, which is a unique feature specific to this region. In South Korea, the infection rate of H1N1pdm09 in wild boar was significantly higher than that of other influenza viruses such as swine H1N1 and H1N2. Specifically, a 2012 study found that among 1,011 samples, H1N1pdm09 was the most prevalent with nine cases (0.9%), followed by swine H1N1 with two cases (0.2%),

and H1N2 with one case (0.1%) (Cho et al., 2015). In contrast, countries such as Italy, the USA, and Japan have reported higher incidence of H1N1 and H1N2 compared to H1N1pdm09 (Prosperi et al., 2022, Martin et al., 2017, Shimoda et al., 2017). These differences may be influenced by factors such as local wildlife ecology, climate, and wildlife management and agricultural practices.

The increase in the seroprevalence of the H1N1pdm09 virus in wild boar can be attributed to the increase in the density of wild boar in urban areas. The average wild boar density per km² around cities increased from 1.51 animals

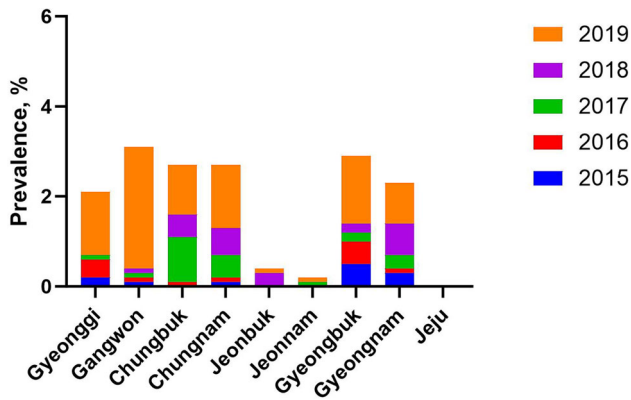


Figure 3. Annual ELISA-based prevalence of Influenza A viruses in wild boar by region in South Korea, 2015–2019.

in 2019 to 3.0 animals in 2020 (Jo et al., 2019; Seo et al., 2020). This may result in increased human–wild boar contact and increased exposure to the H1N1pdm09 virus. Furthermore, in this study Gangwon-do had the highest seroprevalence rate for the H1N1pdm09 virus in swine in 2019, at 1.4%. In that year, Gangwon-do had the largest wild boar population in the country, with an estimated average of 22,583 wild boars (with a maximum of 37,632) (Jo et al., 2019). This suggests that the spread of wild boar influenza viruses in these areas may have resulted in endemic outbreaks, which could have contributed to the increase in seroprevalence in the area.

Another significant observation in this study is the increased cross-reactivity to several viruses, including the H1N1pdm09 influenza virus. This suggests that wild boars may be exposed to multiple virus variants, but could also be a result of antigenic variation in the influenza virus. Nevertheless, such cross-reactivity can be interpreted as an important indicator that may facilitate the emergence of new viral strains that are adaptable to human hosts. In particular, this process of viral adaptation has been documented in domestic swine populations following the 2009 H1N1 pandemic, where continuous genetic recombination among swine influenza viruses post-pandemic has led to the sporadic emergence of strains capable of infecting humans (Chauhan and Gordon, 2020). The observation of several recombinant viruses in domestic swine suggests the potential for similar recombination events in wild boar populations (Kim et al., 2014; Pascua et al., 2013a; Pascua et al., 2013b). The case of a recombinant H1N2 virus, containing genetic segments from the pandemic H1N1, found in Brazilian wild boars further emphasizes this possibility (Biondo et al., 2014). Therefore, definitive confirmation of such multiple infections requires further

investigation through virus isolation and molecular biology techniques. Such studies are crucial for a deeper understanding of the mechanisms of virus transmission and evolution.

In the current study, a seropositivity rate of 0.10% (7 out of 7209 cases) for sH3N2v was detected in wild boar serum samples from South Korea, representing the first identification of this strain in the country following its positive identification in the US. Notably, in the the US, sH3N2v has been documented in both domestic swine and human populations. Although the seropositivity rate for sH3N2v in Korean wild boar is relatively low, it does not completely rule out the possibility of virus transmission through interspecies contact between wild boar and domestic swine or through human–wildlife interactions. The prior confirmation of sH3N2v infections in domestic swine populations in Korea requires increased vigilance regarding the dynamics of virus transmission and the associated risks.

The results of avian virus infection rates in wild boar were consistent with previous findings in other countries. A study by Luo et al. (2013) in China reported negative results for both H5 and H9 avian influenza viruses in wild boar (0/31). Similarly, a study by Vittecoq et al. (2012) in France found no presence of influenza-specific antibodies in serum samples collected from 20 wild boars living in areas with migratory bird populations. However, it is important to note the presence of 100 “indeterminate” that tested positive by ELISA but was not confirmed in the HI test. Given that wild birds can harbor a variety of subtypes, further testing of a wider range of virus subtypes could potentially lead to the identification of additional positive cases, as evidenced by a study conducted in the US that tested a wider range of avian subtypes (H1–H14) and resulted in the detection of 16 avian IAV-positive samples (Martin et al., 2017).

Korea, which is located on the East Asian–Australasian Migratory Flyway, a major bird migration route, is inhabited by various migratory bird species (Li et al., 2019; Hwang et al., 2017). Despite ongoing efforts to control the spread, highly pathogenic avian influenza continues to affect poultry in Korea (Yoo et al., 2022), and cases of direct transmission from wild birds to domestic swine have also been documented (Choi et al., 2013). Therefore, it is of utmost importance to maintain sustained and vigilant surveillance for avian viruses in wild boar.

The present study also reports for the first time the results of serologic testing for canine H3N2 influenza virus

in wild boar serum samples. All samples tested were found to be negative for the virus. Despite this finding, the significance of this study is that it is the first to evaluate the presence of this virus in wild boar. Dogs and wild boar are known to have close contact with each other, with dogs sometimes hunting and consuming raw meat from wild boar. It has been documented that diseases such as brucellosis, Aujeszky's disease, and leptospirosis can be transmitted between dogs, particularly hounds, and wild boars (Ciarello et al., 2022; Woldemeskel, 2013; Cilia et al., 2021). However, there are no previous data on influenza virus exposure between these species. The canine H3N2 influenza virus of avian origin was first identified in South Korea (Song et al., 2008) and has since spread widely among dogs both in Korea and worldwide (Li et al., 2010; Jeoung et al., 2013; Lee et al., 2016). The virus is also capable of naturally infecting cats and has been experimentally shown to infect a variety of mammals including chickens, ferrets, guinea pigs, and mice (Klivelyeva et al., 2022). Given this information, it is of critical importance to continuously monitor the potential exposure of wild boars to this virus.

This study used a large dataset of 7209 samples to investigate the role of wild boar in influenza virus transmission. The use of a high antibody titer threshold (1:40) improved the accuracy of the results, although the impact of genetic diversity and environmental factors in wild boar must also be considered. In particular, the results show an increasing trend in exposure to multiple influenza virus infections over time, including pH1N1. This indicates a progressive increase in seropositivity rates among wild boars in Korea, suggesting their potential role as new vectors and hosts in the transmission of influenza viruses. Such findings are crucial for reconsidering management and surveillance strategies for wild boar and contribute significantly to deepening our understanding of disease transmission between livestock and wildlife. This study provides essential baseline information for the development of these surveillance and management strategies and provides important insights for future research directions.

CONCLUSION

Based on the results of a large-scale, long-term study, this study confirms that wild boars in Korea have been exposed to multiple strains of influenza A virus (IAV), including the H1N1pdm09 strain. Infections with more than one IAV strain were detected in some sera, and an increasing trend

was observed over time. This suggests that wild boar may act as a novel mixing vessel, facilitating the adaptation of IAV and potentially spreading them to other hosts, including humans. Therefore, regular and frequent surveillance of influenza viruses in wild boar is highly recommended.

FUNDING

This work was supported by an international cooperation program managed by the National Research Foundation of Korea(NRF-2019K1A3A1A61091813). Additional funding was provided by the Natural Products Research Institute.

DECLARATION

CONFLICT OF INTEREST The authors declare that they have no competing interest.

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