Submitted: 12/05/2022

Accepted: 12/08/2022

Published: 15/09/2022

Influenza A viruses circulating in dogs: A review of the scientific literature

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Abstract

Influenza A viruses (IAV) cause persistent epidemics and occasional human pandemics, leading to considerable economic losses. The ecology and epidemiology of IAV are very complex and the emergence of novel zoonotic pathogens is one of the greatest challenges in the healthcare. IAV are characterized by genetic and antigenic variability resulting from a combination of high mutation rates and a segmented genome that provides the ability to rapidly change and adapt to new hosts. In this context, available scientific evidence is of great importance for understanding the epidemiology and evolution of influenza viruses. The present review summarizes original research papers and IAV infections reported in dogs all over the world. Reports of interspecies transmission of equine influenza viruses H3N2 from birds to dogs, as well as double and triple reassortant strains resulting from reassortment of avian, human, and canine strains have amplified the genetic variety of canine influenza viruses. A total of 146 articles were deemed acceptable by PubMed and the Google Scholar database and were therefore included in this review. The largest number of research articles (n = 68) were published in Asia, followed by the Americas (n = 44), Europe (n = 31), Africa (n = 2), and Australia (n = 1). Publications are conventionally divided into three categories. The first category (largest group) included modern articles published from 2011 to the present (n = 93). The second group consisted of publications from 2000 to 2010 (n = 46). Single papers of 1919, 1931, 1963, 1972, 1975, and 1992 were also used, which was necessary to emphasize the history of the study of the ecology and evolution of the IAV circulating among various mammalian species. The largest number of publications occurred in 2010 (n = 18) and 2015 (n = 11), which is associated with IAV outbreaks observed at that time in the dog population in America, Europe, and Asia. In general, these findings raise concerns that dogs may mediate the adaptation of IAVs to zoonotic transmission and therefore serve as alternative hosts for genetic reassortment of these viruses. The global concern and significant threat to public health from the present coronavirus diseases 2019 pandemic confirms the necessity for active surveillance of zoonotic viral diseases with pandemic potential.

Keywords: Reassortment, Canine influenza, Equine influenza, Epizootology, Zoonotic infection.

Introduction

The number of new infectious diseases in the world is growing and they pose a serious threat to wildlife, domestic animals, and human health (Jones *et al.*, 2008). According to estimates from the Center for Disease Control and Prevention, influenza is the most widespread infections from over 335 human diseases that have occurred over the past 60 years, causing up to 650,000 deaths per year (https://doh.wa.gov/publichealth-healthcare-providers/public-health-systemresources-and-services/immunization/influenza-fluinformation, 2021).

Unique variability, which is based on both point mutations characteristic of RNA viruses and gene reassortment, largely determines the global and uncontrolled spread of Influenza A viruses (IAV). Eight segments of negative single-stranded RNA [PB2, PB1, PA, hemagglutinin (HA), NP, neuraminidase (NA), M, and NS] make up the IAV genome (Shaw and Palese, 2013). The surface antigens HA and NA are the most variable structural components of the virion. They play an important role in the initial stages of a cellular infection, since it is against them that protective antibodies are produced in the host organism (Nakatsu *et al.*, 2018).

The IAV subtypes are classified based on the antigenic properties of their surface proteins. There are currently 18 HA subtypes and 11 NA subtypes. Despite the extreme variability of IAVs, two viruses with the same subtype can only be distantly related. However, all IAVs are similar enough for possible reassortment by swapping parts of the gene. This allows progeny to be created with elements from both parent viruses unrelated to their original specificity or host subtype. It is known that wild birds are the main natural

reservoir of IAV, since all known subtypes of the virus in the world have been found in wild birds (Herfst *et al.*, 2014). IAV most commonly occurs as an endemic

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infection of the gastrointestinal tract in bird populations that congregate in salt or fresh water (Yoon et al., 2014). Spread of avian IAV infection has been periodically observed in ground bird populations such as domestic turkeys or chickens (Bunpapong et al., 2014). In addition, avian IAV, overcoming the interspecies barrier, can cause epizootic and panzootic infections in various mammalian species (Wright and Webster, 2001; Crawford et al., 2005). Thus, it was noted that, in addition to humans horses, pigs, seals, minks and humans have been noted to have experienced long-term outbreaks and persistent epidemics (Waddell et al., 1963; Guo et al., 1992; Harder and Vahlenkamp, 2010; Song et al., 2012; Krog et al., 2015; Zhao et al., 2019; Chauhan and Gordon, 2020; Husain, 2020; Saktaganov et al., 2020; Klivleyeva et al., 2021a, 2021b; Chauhan and Gordon, 2022), but influenza infection in dogs has not been well studied until recently (Lyu et al., 2019). In recent years, there have been reports of IAV infection in dogs and cats (Parrish and Voorhees, 2019; Borland et al., 2020). Thus, interspecies transmission is one of the important ecological and epidemiological features of IAV (Chauhan and Gordon, 2021).

The main points in the evolution of IAV are mutations and reassortment. IAV, like other RNA-containing viruses, has a high mutation rate due to the absence of the modification activity of the viral polymerase (Sanjuan et al., 2010). In addition, reassortment of segments permits to rapidly initiate genetic traits end block. It is significant that both processes (mutation and reassortment) are connected with interspecies transmission and the appearance of the influenza virus. An example of this is the transmission of IAV from horses to dogs-mutation (Dundon et al., 2010) and the spread of the H1N1 virus from swine to humans (2009 influenza pandemic)-reassortment (Lin et al., 2012). A detailed understanding of IAV dates back to 1918, when the H1N1 virus appeared, causing parallel pandemics in humans and pigs (Shope, 1931a, 1913b; Koen, 1919). From the 20th century on, pandemic IAVs occurred in humans in 1918 and then in 2009 after transferring whole viruses from other hosts. However, in 1957 and 1968, pandemic variants of these viruses circulated in humans after replacement of the third and second viral gene segments from avian sources of the virus (Pulit-Penaloza et al., 2017). In addition, many other cases of bird-to-human (or other animal) transmission or small outbreaks have been described which can cause severe infections with little or no other transmission (Choi et al., 2005; Peiris et al, 2007; Amonsin et al., 2007; Takano et al., 2009; Zhao et al., 2019; Lewis et al, 2021).

However, although IAVs have been consistently spread in humans as well as in other mammals (Songserm *et al.*, 2006; Dundon *et al.*, 2010; Lin *et al.*, 2012), dogs have always been considered immune to IAV, because outbreaks of IAV in the population of dogs were not found. Though, two canine influenza viruses (CIV) have emerged, both of equine and avian origin (Crawford *et al.*, 2005; Song *et al.*, 2008). The first cases of CIV-H3N8 were reported in the United States. Phylogenetic analysis established that AIV H3N8 originated from the IAV H3N8 equine variant, as all eight segments were closely related to segments of the equine influenza virus (EIV) that were circulating at the same time (Crawford *et al.*, 2005). CIV-H3N8 is currently an enzootic disease in the USA (Hayward *et al.*, 2010; Pecoraro *et al.*, 2014a). Efficient H3N8 and H3N2 avian influenza circulation in dog populations has been observed in the Americas, Europe, and Asia (Harder and Vahlenkamp, 2010). There are also reports of isolation of H3N2 avian influenza virus from dogs in northern China (Sun *et al.*, 2013b).

IAV and the circulation of CIV

Regardless of the fact that waterfowl are considered to be natural host for many IAVs, a significant number of avian IAVs possess specificity to the host and are not pathogenic to humans. Dogs are among the most popular companion animals worldwide, their number exceeds 900 million (Coppinger and Coppinger, 2001; Wasik *et al.*, 2021). Considering that in some countries dogs are used both as pets and for work and even as a food source, it can be assumed that they might become, like pigs, another "mixing vessel" in which avian, human, and CIV are able to repeatedly reassort and give rise to new viruses with pandemic potential. They can therefore pose a significant risk to health of human as carriers of influenza virus.

CIV belongs to the influenza viruses of the genus IAV within the Orthomyxoviridae family (Shaw and Palese, 2013; Nogales *et al.*, 2019) and can be caused by two subtypes: A/H3N2 avian-origin influenza virus and A/H3N8 EIV (Payungporn *et al.*, 2008). Both of these influenza virus variants have been circulating continuously among the canine population since they were first reported in 2000 in various animal species (Payungporn *et al.*, 2008; Gibbs and Anderson, 2010). *H3N8 CIV*

Epizootics of IAV in populations of dogs have occurred relatively recently (Crawford et al., 2005; Pulit-Penaloza et al, 2017). There are several early reports of the existence of antibodies against human IAV in dogs and the ability to elicit an antibody response in dogs when infected with human influenza virus (Nikitin et al., 1972; Kilbourne and Kehoe, 1975). However, the first mentions of the transmission of A/H3N8 EIV to dogs appeared approximately in 1999 in Florida, USA (Coppinger and Coppinger, 2001; Crawford et al., 2005; Parrish et al., 2015). There were no assumptions that dogs might be natural hosts for influenza infection or epidemic spread until 2004. The official beginning of canine influenza was the identification of influenza A/H3N8 virus in greyhounds with respiratory illness in Florida in 2004 (Crawford et al., 2005; Yoon et al., 2005). Infected dogs mostly suffered from mild upper respiratory illness, although some had more severe

disease, including hemorrhagic bronchopneumonia (Crawford *et al.*, 2005; Newton *et al.*, 2007). The virus has been reported to be circulating among dogs in the USA for over a decade with the greatest prevalence in Colorado and the northeastern states (Jirjis *et al.*, 2010; Pecoraro, 2013, 2014b; Pulit-Penaloza *et al.*, 2017; Voorhees *et al.*, 2017).

Subsequently, the A/H3N8 virus, detected in racing greyhounds, became endemic among populations of domestic animals, including dogs. Following initial reports, A/H3N8 EIV has been found in thousands of dogs of various breeds in the United States (Coppinger and Coppinger, 2001; Deshpande et al., 2009a; Anderson et al., 2013). Analysis of sera samples collected from dogs in Florida showed that the first positive sera were obtained in 2000. Serological testing for the presence of antibodies against IAV H3 in blood sera collected in 2004 from greyhounds participating in racing in various training centers and racetracks and dogs from animal shelters, showed up to 100% of seropositive animals at each facility (Crawford et al., 2005, Barrell et al., 2010; Pecoraro et al., 2014a). When examining sera, antibodies were detected in dogs in at least 19 states from 2005 through June 2009 (Anderson et al., 2013). Subsequently, epidemiological studies were also carried out in other countries, as a result of which the information was obtained on the infection of dogs in the immediate vicinity of infected horses (Kruth et al., 2008). Cases of infection of dogs with EIV A/H3N8 in the UK have been described in September 2002 (Daly et al., 2008). In 2007, during a widespread outbreak of equine influenza in Australia, influenza infection was detected in 10 out of 40 dogs examined (Kirkland et al., 2010). It has also been shown that EIV can be experimentally transmitted from infected horses to dogs that have been in contact with them (Yamanaka et al., 2009).

H3N2 CIV

The IAV A/H3N2 has spread widely among dogs in South Korea (Song et al., 2008; Li et al., 2010; Jeoung et al., 2012; Lee et al., 2015). Influenza viruses were isolated in chicken embryos from the swabs collected from dogs that showed features of respiratory disease (Lin et al., 2012b). Genome-wide analysis of isolated strains of IAV H3N2 revealed 95.5%-98.9% homology with avian influenza viruses in East Asia (Kang et al., 2013; Zhu et al., 2015; Lee et al., 2016). Serological studies of blood sera obtained from affected dogs showed a high prevalence of antibodies against the H3N2 virus, indicating dog-to-dog transmission (Song et al., 2009; Lee et al., 2009; Zhao et al., 2011; Horimoto et al., 2014). Additional serological testing in dogs not attached to dog farms or kennels also showed anti-H3N2 antibodies (An et al., 2010).

The avian influenza A/H3N2 virus has spread widely among dogs in several regions of China (Li *et al.*, 2010; Lin *et al.*, 2012b), and also in Thailand in 2012 (Bunpapong *et al.*, 2014). A retrospective serological

study demonstrated the presence of antibodies against canine influenza in animals in Korea in 2005 (Lee *et al.*, 2012). The exact origin of CIV H3N2 is not yet known and phylogenetic analysis of viral sequences shows that viruses isolated in China and Korea are close to the ancestors of a canine lineage (Parrish and Dubovi, 2017; Lyu *et al.*, 2019).

CIV H3N2 has been shown to infect cats and under certain circumstances has caused natural outbreaks in cats in Korea and China (Beeler, 2009; Song et al., 2011; Lei et al., 2012; Jeoung et al., 2013). The genome-wide and phylogenetic analysis of these viruses from cats revealed their similarity with the avian A/H3N2 viruses isolated at the same time from dogs and cats in Korea and China (Su et al., 2013; Lee et al., 2018). Currently, A/H3N2 virus is the prevalent CIV strain, which is widespread not only in Asia, but throughout the world (Murcia et al., 2010; Yang et al., 2014; Voorhees et al., 2018). Experimental infection of various animal species, including chickens, pigs, mice, guinea pigs, and ferrets with the avian-origin A/ H3N2 virus isolated from dogs, showed its complete adaptation for mammals (McKinley et al., 2010; Solórzano et al., 2015). Infection of ferrets with CIV occurred after experimental inoculation (Kim et al., 2013), and some limited natural spread of infection between ferrets was found (Lee et al., 2013b). Reassortant viruses containing segments of the H3N2 virus and other segments of human viruses have been described, including virus containing 7 segments of the pandemic H1N1 virus and HA segment of the canine virus (Song et al., 2012). This indicates the successful implementation of interspecies transmission of the avian influenza A/H3N2 virus to dogs (Deshpande et al., 2009b; Lyoo et al., 2016; Luo et al., 2018). Human influenza viruses circulating in the dog

population

No cases of human infection with any of the CIV subtypes have been reported. However, seasonal subtypes of human IAV can occasionally infect dogs, including the H1N1 strains (original seasonal and 2009 pandemic variants) and seasonal H3N2 viruses (Murcia et al., 2010; Kim et al., 2013; Su et al., 2013; Zhao, 2014; Lee et al., 2018; Voorhees et al., 2018; Borland et al., 2020). Serologic testing of sera samples has revealed signs of pandemic A/H1N1 influenza virus in dogs in Thailand and Italy (Dundon et al., 2010; Song et al., 2012; Pratelli and Colao, 2014; Tangwangvivat et al., 2019), and this virus has also been associated with an outbreak of clinical disease in cats in Italy with 55% seropositivity (Fiorentini et al., 2011). Testing of cats and dogs in Japan using serological tests showed that 3.8% of cats and 2.1% of dogs were positive for antibodies against influenza H3 virus of human origin (Said et al., 2011; Horimoto et al., 2014). Higher numbers of sera positive for pandemic and seasonal IAV H1N1 (20%-50% seropositivity) have been reported in cats in the United States (Ali et al., 2011;

More *et al.*, 2020), and a similar percentage of positive sera samples have been recorded in dogs in the USA (Seiler *et al.*, 2010; McCullers *et al.*, 2011). The reasons for the high proportion of seropositive animals to IAV H1N1 in the United States compared to other countries are unknown, but may be related to the high sensitivity tests used to detect specific antibodies (Gonzalez *et al.*, 2014; Luo *et al.*, 2018).

None of these infections have been further spread to dogs, but they may provide the possibility of re-emergence of human IAV in dogs. The IAV H3N1 isolated from a dog in Korea is the result of a recombination of the CIV H3N2 (HA) and the pandemic H1N1/09 virus (other 7 gene segments) (Sun et al., 2014; Chen et al., 2015, 2018; Na et al., 2015; Jang et al., 2017). Also, reassortant IAV was reconfirmed by the isolation of two reassortant viruses A/H3N1 and A/H3N2 from dogs in South Korea in 2010 and 2012, which inherited genetic material from the human influenza A/H1N1pdm/09 virus and avian-origin A/H3N2 CIV (Song et al., 2012; Hong et al., 2014; Zhang et al., 2015). In 2015, IAV H3N2 isolated from a dog in Korea was reported to be a reassortant containing the PA genomic segment of the avian pandemic H9N2 virus (Chen et al., 2018). Moreover, a similar variety of sialic acid variants and linkages which may be related to differences in IAV infection and host range is observed between humans and dogs (Chen et al., 2015; Song et al., 2015).

Avian influenza viruses circulating in the dog population In 2005–2006, the transmission of an avian-origin A/ H3N2 to dogs has been recorded in Asia (Parrish et al., 2015). There are evidences that the avian influenza A/H5N1, A/H5N2, A/H9N2, A/H10N8 viruses and human A/H1N1pdm/09 virus can also be transmitted to dogs (Songserm et al., 2006; Lin et al., 2012a; Sun et al., 2013; Song et al., 2013; Zhang et al., 2013; Su et al., 2014a; Lee et al., 2016b). In October 2004, a 1-year-old dog with severe respiratory symptoms died in Thailand a few days following the ingestion of a duck infected with the avian influenza H5N1virus (Songserm et al., 2006). The ability of the H5N1 virus to infect mammals was established during the isolation of the H5N1 influenza virus from canine tissues (Amonsin et al., 2007; Maas et al., 2007; Giese et al., 2008).

The avian IAV H5N2 was isolated from a dog in China in 2009 (Zhan *et al.*, 2012). Serological studies on stray dogs that are found frequently in the live poultry markets in China have shown low but consistent presence of antibodies against H9N2, H3N2, and H5N1 viruses (Song *et al.*, 2009; Zhang *et al.*, 2013; Su *et al.*, 2014a, 2014b; Na *et al.*, 2015; Zhou *et al.*, 2015; Brown, 2000). Both dogs and cats can be experimentally infected with the avian influenza H5N1virus (Chen *et al.*, 2010), and infections can also occur after eating meat from infected animals (Lyoo *et al.*, 2017).

Reassortant IAV found in dogs

Since different subtypes of influenza viruses are circulating in the dog population, the chances of

generating reassortant viruses are enhanced. In contrast to A/H3N2 CIV and human influenza A/H1N1pdm/09 virus, which did not cause noticeable disease symptoms in dogs, the resulting reassortant A/H3N1 in infected dogs induced mild symptoms, including fever, cough, sneezing, and lethargy (Hong *et al.*, 2014; Kong *et al.*, 2015). The emergence of reassortant variants in dogs has been confirmed by the circulation of the swineorigin IAV H1N1 with a phenotype that promotes transmission of the virus to humans (Su *et al.*, 2014a; Wang *et al.*, 2019).

In the United States, A/H3N8 CIV has become widespread since 2004 and continued to circulate for several years, but after 2016 it was less frequently detected. In 2015, the IAV H3N2 was reported for the first time in the USA, causing massive disease outbreaks in dogs (Ramirez-Martinez *et al.*, 2013; Parrish and Voorhees, 2019). In Singapore, an outbreak of influenza caused by the avian-origin H3N2 IAV occurred in dog shelters in 2018 (Wang, 2019).

Virus sequence analysis showed that the H3N8 CIV outbreak in the USA was initiated by a virus that was transmitted from horses. The evidence suggests that A/H3N2 has become endemic in dog populations. There was no evidence of reassortment with any other IAV (Hayward *et al.*, 2010; Rivailler *et al.*, 2010).

The CIV lineage quickly deviated from EIV, which continued to circulate in horses, and acquired specific substitutions in each gene segment to form a virusspecific clade for each gene segment. Although the specific properties of canine viruses have not been clearly identified, some of the sequence changes may have been selected for adaptation in dogs (Dubovi and Njaa, 2008; Dubovi, 2010; Hong et al., 2014). Changes within and near the receptor-binding site of the HA1 protein have been shown to alter binding to sulfated glycans and probably induce other changes in sialic acid binding (Collins et al., 2014; Parrish and Dubovi, 2017; Zheng et al., 2018), which may promote viral replication in the dog's respiratory tract. Currently, there is no evidence of the CIV transmission back to horses, and there is likely a barrier to such infections, since CIV isolates ineffectively replicated in experimentally infected horses or cultures of equine tracheal cells (Yamanaka et al., 2010; Quintana et al., 2011; Yamanaka et al., 2012). The H3N8 EIV has also been isolated from swine with clinical disease in China (Song et al., 2008; Tu et al., 2009; Kirkland et al., 2010; Abente et al., 2016; Lyoo et al., 2017), as well as from bactrian camels (Yondon et al., 2014).

Clinical signs and prevention

The CIV most often causes respiratory disease with usually mild or subclinical symptoms, although sometimes an infection can be severe. A mild illness is associated with sneezing, cough, which is usually moist and accompanied by nasal discharge, as well as anorexia. Symptoms may last 7–10 days, and animals usually recover without complications. Dogs with more severe illness may have a high fever (over 42° C) with dyspnea and other signs of pneumonia, and disease symptoms develop very quickly. The virus is detected in various respiratory tissues, and infection of the trachea, bronchi, and lungs is frequently observed (Castleman *et al.*, 2010; Parrish and Dubovi, 2017). Often the disease is aggravated by a bacterial infection of the lungs. The severity of the disease depends on the specific circumstances of the infection, and symptoms may be aggravated by co-infections with other pathogens.

Close contact with influenza-susceptible animals accelerates the spread of the infection. The main infection control measures include isolation of infected animals, disinfection of animal cages and various fomites, as well as sanitary and hygienic measures. Clothes can be cleaned with detergent if the washing cycle is followed (Parrish and Dubovi, 2017). To keep canine flu outbreaks under control, dog owners should contact their veterinarian if their pet shows signs of a respiratory illness.

IAV appear to require relatively close contact for transmission; that is why viruses do not persist in most domestic dog populations for long periods. However, viruses can sometimes continue to spread for longer periods of time in large animal shelters, kennels or dog meat farms in Asia (Smith *et al.*, 2005). It is very important in this case to keep the quarantine and isolation of infected animals, which will reduce the spread of the virus inside the facility between animals and people.

A number of vaccines have been developed against the CIV subtypes H3N8 and H3N2. These include various inactivated viral vaccines that reduce symptoms of infection and clinical manifestations of disease when given two doses with a 3-week interval (Crawford *et al.*, 2005; Kirkland *et al.*, 2010; Hong *et al.*, 2014; Parrish and Dubovi, 2017; Wasik *et al.*, 2021). These vaccines are generally recommended for dogs at high risk of respiratory infections, but are currently not given routinely to most domestic dogs. Experimental canarypox-vectored virus vaccines that express the HA proteins of EIV or CIV have been shown to be effective in reducing viral replication and disease severity in dogs (Karaca *et al.*, 2007; Castleman *et al.*, 2010; Larson *et al.*, 2011; Lee *et al.*, 2013a).

Discussion

Over the past 16 years, IAV H3N2 and H3N8 have emerged in sporadic cases and spread epidemically among a variety of dog populations. In addition, other, more limited outbreaks of the disease in dogs have been reported, and there have also been cases when canine viruses have transmitted infections to other hosts, including cats. In addition, there is growing evidence of low but persistent rates of infection in dogs with some circulating seasonal human and avian influenza viruses, albeit with likely minor or no illness (Dalziel *et al.*, 2014). Since dogs are often exposed to viruses from other animals, there appear to be significant barriers to interspecies infection, but under some circumstances these barriers can be overcome by means of different types of influenza viruses (Murcia *et al.*, 2011).

To date, there have been no reports of human infection with CIV. However, precautions should be taken and all cases of influenza infection in both human and dogs should be reported to medical staff. Contact with sick animals is contraindicated for people at risk such as people with a weakened immune system, the elderly, young children, and pregnant women.

In view of the current coronavirus diseases 2019 pandemic originated in China, the presence of avian influenza virus strains in dogs in China should be viewed as a significant threat to the future. Strengthening of the epidemiological surveillance to address public concerns about pandemic influenza viruses will undoubtedly lead to the detection of new cases of influenza virus infection in dogs. Each newly emerging infection provides an opportunity for appearing a unique variant and continuing the evolution of the IAV as a causative agent of interspecies crossing.

Controlling influenza infection in the dog population is therefore important for both dog's health and human well-being and will be useful in updating existing diagnostic protocols and vaccines to prevent future outbreaks of influenza virus (Lee *et al.*, 2012).

Conclusion

CIVs A/H3N2 and A/H3N8 cause upper respiratory tract diseases in dogs lasting several days or more. The viruses seem to require relatively close contact to give transmission, so transmission of the virus among dogs is especially easy in group housing settings such as animal shelters and boarding kennels. Under these conditions, due to the ongoing genetic changes, new strains of the influenza virus may appear in dogs, which can become a source of infection for other animals and humans. Close contact of dogs with humans may be a cause of the zoonotic potential of influenza viruses and contribute to the infection of dogs with human influenza viruses. They can also be infected both from other domestic animals and from wild birds. Vaccinations provide a level of protection against CIV infection or disease, and should be given to animals that are likely to be exposed, or that are predisposed to more severe disease by comorbidities or other factors.

Conflict of interest

The authors declare that there is no conflict of interest. *Funding*

The article was funded by grant 325/1 of the program "Development and application of new technologies of genomic and bioinformatic analysis, contributing to the conservation of biodiversity, increasing the productivity of animals and plants, protecting organisms from the damaging effects of mutagens and improving the quality of life of the population" provided by the Ministry of Education and Science of the Republic of Kazakhstan. *Authors' contribution*

All authors have equal contributions.

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