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Avian influenza virus ecology in wild birds of Western Siberia

K. A. Sharshov[1*], A. K. Yurlov[2], Xinxin Li[3], Wen Wang[4], Laixing Li[4], Yuhai Bi[5], Wenjun Liu[6], Takehiko Saito[7], Haruko Ogawa[8] and A. M. Shestopalov[1]

Abstract

Background: The aim of the study was to explore the ecological diversity of wild birds in Siberia, which are the natural reservoir of avian influenza virus (AIV).

Methods: Cloacal swabs and intestinal fragments were collected from wild migratory birds from 2007–2014. Isolated viruses were grown in the allantoic cavity of embryonated chicken eggs. The presence of virus was determined using hemagglutination assays. Primary identification and subtyping of influenza viruses was confirmed by RT-PCR.

Results: A total of 2300 samples obtained from wild migratory birds of 8 orders were collected and tested. Influenza was detected in 185 birds of 3 orders. Species of family Anatidae (order Anseriformes) such as European Teal (*Anas crecca*), Garganey Teal (*A. querquedula*), and Shoveler (*A. clypeata*) play the main role in AIV circulation in the south of Western Siberia. The proportion of viral carriers among waterfowl ranged from 5.6 to 20% in 2007–2014. The order Charadriiformes had lower virus isolation rates of not more than 1.4%.

Conclusions: Wild migratory waterfowl of orders Anseriformes and Charadriiformes are the main reservoir of AIV in the south of Western Siberia. This area plays a key role in persistence, evolution, and geographical distribution of avian influenza.

Keywords: Influenza A virus, Wild birds, Water and wetland complex, Ecology, Migration, Distribution, Surveillance

Background

Influenza is an animal and human disease caused by the following genera of Orthomyxoviridae family: influenza virus A, influenza virus B, influenza virus C. Among them, only influenza A viruses have a wide range of hosts with waterfowl being the main hosts. Influenza A viruses are also isolated from pigs, horses, dogs, rodents, some marine mammals, cats, minks, and humans (Webster et al. 1992).

The diversity of avian influenza viruses (AIV) is maintained by wild birds, which are the natural reservoir of influenza (Stallknecht and Shane 1988; Neumann and Kawaoka 2006). Anseriformes and Charadriiformes play a leading role in the natural circulation of influenza viruses. Anseriformes and Charadriiformes are long-distance migrants, and some species can cover up to several thousand kilometers and carry the virus over long distances, which is very important in terms of influenza epidemiology (Erohov 1988).

The life cycle of Anseriformes and Charadriiformes includes stopover on water bodies where a great number of birds from various regions can gather during migration. This can result in the active exchange of influenza viruses, reassortment, the emergence of new variants, and their further spread. Influenza infections follow a seasonal pattern and usually peak in late autumn (Dowell 2001). This may be caused by the presence of many naive young birds in bird populations in autumn. Direct or indirect contacts between wild waterfowl and poultry are also very important as they usually result in influenza transmission and poultry outbreaks (Downie et al. 1977). Seasonal migrations of wild birds promote the spread of multiple influenza A viruses to distant areas and provide

*Correspondence: sharshov@yandex.ru
[1] Laboratory of Experimental Modeling and Pathogenesis of Infectious Diseases, Research Institute of Experimental and Clinical Medicine, Novosibirsk, Russia 630117
Full list of author information is available at the end of the article

their long-term persistence in various ecosystems. It is therefore important to conduct the AIV surveillance in natural conditions.

Water appears to be the optimal medium to maintain and transmit influenza viruses in nature, which explains the wide spread of this pathogen in waterfowl. In fresh water, the virus can retain infectivity for up to 4 days at 22 °C, for more than 30 days at 0 °C, and for a much longer period in ice and frozen soil (Rogers et al. 2004). It is likely that infected birds shed the virus in their feces. The virus gets into cold water and soil and persists for a whole winter. In spring, when birds come back, they are exposed to melted water and soil and reinfected (Marchenko et al. 2010a, b).

The main breeding grounds of many migratory Anseriformes and Charadriiformes are located in the north of Russia. The West Siberian Plain is a territory of particular importance (Gilbert et al. 2006; Sharshov et al. 2007, 2010; Donchenko et al. 2010) as there are a lot of rivers and lakes in the south of Western Siberia that are situated on migratory routes and serve as breeding grounds for many species that are ecologically connected with water bodies. Lake Chany is the biggest lake of the region and is known to be the site of the largest migratory stopover of birds (Veen et al. 2005). The south of Western Siberia is crossed by several significant flyways, namely, Central Asian Flyway, Asian–East African Flyway, and East Asian–Australasian Flyway. These flyways unite the populations of birds wintering in different regions such as Europe, Africa, Middle East, Central Asia, India, South-East Asia, Australia, and Oceania. These conditions favor the wide spread of different influenza viruses and the study of influenza A ecology in the south of Western Siberia. Such study may help to understand the reasons behind wide genetic diversity of influenza A viruses and the spread of this pathogen in Eurasia (Sharshov et al. 2011; Zaykovskaya et al. 2011).

Methods

We conducted regular AIV surveillance in the south of Western Siberia. Cloacal swabs were collected from hunt-harvested wild birds or from wild birds captured using nets during spring and autumn migration. The samples were taken using dry cotton swabs and put into numbered vials with sterile transport medium. One-mL portions of prepared medium were packed in sterile 2-mL plastic vials. All procedures (component mixing and packing) with medium were performed under sterile conditions. Vials with medium were stored at +4 °C or room temperature for not more than 2 days. If a longer storage was necessary, vials were stored at –20 °C. Collected samples were stored in liquid nitrogen or freezer at ≤–70 °C before analysis.

Virus isolation

AIV isolation from cloacal swabs was performed in embryonated chicken eggs using three serial passages according to the WHO procedure and the national training course on animal influenza diagnosis and surveillance of China. After each passage, allantoic fluid was tested for hemagglutination activity in hemagglutination assay.

Hemagglutination assay

Two-fold serial dilutions of tested allantoic fluid were prepared in 96-well plate using phosphate-buffered saline. Final volume of diluted allantoic fluid in each plate was 50 μL. A volume of 50 μL of erythrocyte suspension was added to each well and mixed by pipetting. Plates were incubated for 30 min at 4 °C before reading. The presence of hemagglutinating agents in samples of allantoic fluid was determined by suspended distribution of erythrocytes, and HA was considered positive. The well with last two-fold dilution, where HA was still positive, was considered as titration end point. The haemagglutination titre of the allantoic fluid was the reciprocal of this dilution. One hemagglutinating unit (HAU) was defined as the amount of AIV in titration end point. For hemagglutination inhibition assay, virus-containing allantoic fluid was diluted to 4 HU in 25 μL of fluid.

PCR amplification and sequencing

Viral RNA was isolated from allantoic fluid using SV Total RNA Isolation System (Promega Corporation, USA). Uni12 universal primers and AMV-reverse Transcriptase (Fermentas, Lithuania) were used for reverse transcription. Gene-specific primers were used for PCR. Amplicons were extracted using QIA quick gel extraction kit (Qiagen, USA). RNA extraction, reverse transcription, amplification, and amplification product purification were performed in accordance with manufacturer's protocols. Previously described primers were used for subtyping (Hoffmann et al. 2001).

Results

Biological diversity of AIV in wild birds in the south of Western Siberia was studied in 2007–2014. Annual field works were carried out during spring and autumn migration of wild birds to collect biological material. A total of 2300 samples from wild birds of the following 8 orders were collected: Anseriformes, Charadriiformes, Passeriformes, Ciconiiformes, Gruiformes, Podicipediformes, Pelecaniformes, and birds of prey. Majority of samples were collected from birds of 3 orders: Anseriformes, Charadriiformes, and Passeriformes. Samples from Anseriformes accounted for more than 70% of the total number, which is due to preferred sampling of birds from water and wetland ecological complexes. Sampling

preferences were determined by literature data suggesting that Anseriformes play a pivotal role in AIV circulation. Most sampled birds belonged to Anseriformes and were represented primarily by wild ducks such as Garganey Teal (*Anas querquedula*), European Teal (*Anas crecca*), Pochard (*Aythya ferina*), Mallard Duck (*Anas platyrhynchos*), Gadwall (*Anas strepera*), and Shoveler (*Anas clypeata*). The number of studied Anseriformes samples is shown in Table 1.

These bird species are the most widespread in the south of Siberia and migrate there for nesting. They are considered the main natural reservoir of AIV. A total of 185 AIV isolates were obtained from biological material collected from Anseriformes. The following species dominate among Anseriformes from which AIV was isolated: Garganey Teal, European Teal, and Shoveler. The percent of viral carriers among Anseriformes ranged from 5.6 to 20% in this period (Table 2).

There were also a lot of Charadriiformes among the sampled birds. A total of 556 Charadriiformes were sampled. The most frequent sampled species, which belong to family Laridae, were Common Gull *(Larus canus)*, Black-headed Gull (*L. ridibundus*), and European Herring Gull (*L. argentatus*). These species accounted for more than 65.55% of sampled Charadriiformes. A significant number of sampled birds belong to family Scolopacidae (waders, peewit, Ruff *Calidris pugnax*, Black-tailed Godwit *Limosa limosa*, and curlew) and accounted for 21.04% of sampled Charadriiformes. Although there were few birds of other Charadriiformes species, it is important to study these species as carriers of the virus to determine the host range of AIV.

Discussion

Our findings suggest that wetland birds, namely Anseriformes, play a key role in the maintenance of natural AIV circulation. We compared the numbers of AIV carriers within wild bird populations in the south of Western Siberia in 2007–2014. European Teal is one of the most widespread species of Anseriformes in the south of Western Siberia. European Teal winters in western Europe, the Mediterranean, and the Caspian Sea. Various subtypes (H1N1, H2N1, H3N8, H4N6, H5N1, H8N4, H8N4, and H15N4) were isolated from European Teals during influenza surveillance in Russian Federation (Sivay et al. 2011, 2013, 2014; Marchenko et al. 2010a, 2012a, b; Donchenko et al. 2012; Sharshov et al. 2012; Sayfutdinova et al. 2012). Lower virus isolation rates are typical for Charadriiformes (Webster et al. 1992; Stallknecht and Shane 1988; Neumann and Kawaoka 2006). In our study, the percent of viral carriers among Charadriiformes was 1.4%. Literature data suggest that AIV isolation rate in Charadriiformes ranges from 0.51 to 10.07% (Hurt et al. 2006; Germundsson et al. 2010). The AIV isolation rate for Coot (*Fulica atra*), which was the only sampled member of the order Gruiformes, was 2.6%.

Our findings demonstrate that the highest percent of viral carriers among Anseriformes was reported in 2012

Table 1 Sampled wild birds (Anseriformes) in the south of Western Siberia by species

Species	2007	2008	2009	2010	2011	2012	2013	2014	Total number
Garganey Teal (*Anas querquedula*)	90	79	36	52	48	2	16	52	375
European Teal (*Anas crecca*)	89	74	29	34	41	25	27	34	353
Pochard (*Aythya ferina*)	65	29	30	38	81	16	24	35	318
Mallard Duck (*Anas platyrhynchos*)	57	24	17	16	27	16	41	29	227
Gadwall (*Anas strepera*)	37	25	23	22	10	9	27	18	171
Shoveler (*Anas clypeata*)	33	30	6	8	16	8	16	42	159
Pintail (*Anas acuta*)	3	15	0	4	2	2	3	8	37
Tufted Duck (*Aythya fuligula*)	2	3	1	0	4	2	3	4	19
Wigeon (*Anas penelope*)	5	0	0	4	0	0	0	0	9
Common Goldeneye (*Bucephala clangula*)	0	0	0	3	2	0	0	4	9
Smew (*Mergellus albellus*)	4	0	0	0	0	0	0	2	6
White-headed Duck (*Oxyura leucocephala*)	0	0	0	0	1	0	0	1	2
Total number	385	279	142	181	232	80	157	229	1685

Table 2 AIV isolation from Anseriformes in 2007–2014

Year	2007	2008	2009	2010	2011	2012	2013	2014
Isolation rate (%)	15.6	8.2	7.7	5.6	6	20	7	14.8

and 2014, which may be related to climatic conditions. In particular, aquatic conditions (hydrological regime of water bodies, seasonal dryness, etc.) are most important for Anseriformes. Migration period in each year is also very important for AIV transmission and influences the density of migratory birds in gathering sites. Mass gatherings of birds are occasionally observed in some habitats in spring and autumn. A number of species form monospecies and multispecies colonies consisting of several thousand birds during nesting period. Local gatherings including up to 50 species and more than 20,000 birds at a time occur in post-nesting periods and during flight. Mass gatherings involve contacts between different species or populations and create conditions that favour the spread of viral and infectious diseases (Downie et al. 1977; Webster et al. 1992; Veen et al. 2005; Neumann and Kawaoka 2006; Marchenko et al. 2010a, b).

Phylogenetic analysis of M gene of all AIV strains isolated in the study has shown that the viruses are avian-like. The following two main groups of viruses can be distinguished: avian influenza viruses of Eurasian lineage (Eurasian clade) and gull influenza viruses. In terms of isolation dates, all viruses on M gene phylogenetic tree are chaotically positioned, which is suggestive of persistence of different M gene lineages in populations of wild birds in the south of Western Siberia. Phylogenetic analysis shows that avian-like viruses circulate in the south of Western Siberia in wild birds of orders Anseriformes, Ciconiiformes, Gruiformes, and Charadriiformes. Gulls are one of the main reservoirs of low pathogenic avian influenza A viruses. However, mechanisms of transmission and maintenance of certain influenza subtypes in gull populations remain poorly understood. Despite the fact that most existing influenza subtypes were isolated from gulls, only two hemagglutinin subtypes (H13 and H16) mainly circulate in gulls, and available evidence of multiple observations suggest that in nature these two subtypes are primarily maintained in gull populations (Fouchier et al. 2005). It has been shown recently that gull influenza viruses have specific gene pool and undergo frequent gene reassortment (Sharshov et al. 2014a, b).

The south of Western Siberia is located in the center of Eurasia, crossed by three main flyways of migratory birds and unites the migratory flyways of European, African, Asian, and Oceanic birds (Veen et al. 2005). The climate of the region favors prolonged viral persistence in soil and water (Sivay et al. 2012a, b; De Marco et al. 2014).

Conclusions

Western Siberia plays an important role in persistence, evolution, and geographical spread of avian influenza viruses. Our findings warrant further influenza surveillance program in wild birds of Western Siberia belonging to different taxonomic and ecological groups. This study may bring valuable data on influenza diversity, evolution, and geographical spread.

Authors' contributions

KAS and AMS conceived and designed the experiments. KAS, XL, WW, and AMS performed the experiments. KAS, WW, LL, YB, WL, TS, and HO analyzed the data. KAS, XL, and AMS contributed reagents/materials/analysis tools. KAS, WW, LL, YB, WL, TS, and HO wrote the paper. KAS, AKY, XL, and AMS collected data and biological samples. KAS, WW, LL, YB, WL, TS, and HO contributed to fruitful discussion and critical revision of the manuscript. All authors read and approved the final manuscript.

Author details

[1] Laboratory of Experimental Modeling and Pathogenesis of Infectious Diseases, Research Institute of Experimental and Clinical Medicine, Novosibirsk, Russia 630117. [2] Research Group of Birds Ecology, Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia 630091. [3] Faculty of Natural Sciences, Novosibirsk State University, Novosibirsk, Russia 630090. [4] Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China. [5] Center for Influenza Research and Early-warning (CASCIRE), Chinese Academy of Sciences, Beijing 100101, China. [6] CAS Key Laboratory of Pathogenic Microbiology and Immunology (CASPMI), Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China. [7] Division of Transboundary Animal Disease, National Institute of Animal Health (NIAH), National Agriculture and Food Research Organization (NARO), Tsukuba, Ibaraki 305-0856, Japan. [8] Diagnostic Center for Animal Health and Food Safety, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan.

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Competing interests

The authors declare that they have no competing interests.

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References

De Marco MA, Delogu M, Sivay M, Sharshov K, Yurlov A, Cotti C, Shestopalov A. Virological evaluation of avian influenza virus persistence in natural and anthropic ecosystems of Western Siberia (Novosibirsk Region, summer 2012). PLoS ONE. 2014;9:e100859.

Donchenko AS, Yushkov YuG, Marchenko VYu, Sharshov KA, Alexeyev AYu, Ilyinykh FA, Savchenko IA, Karpova NV, Savchenko AP, Shestopalov AM. Results of influenza virus surveillance in wild birds in Krasnoyarsk Territory (2008). Sib Herald Agric Sci. 2010;7:61–7 **(in Russian)**.

Donchenko AS, Yushkov YuG, Sivai MV, Sharshov KA, Shestopalov AM, Gulyaeva MA. Genotyping of influenza A viruses isolated from wild birds in the south of Western Siberia in 2011. Sib Herald Agric Sci. 2012;6:84–9 **(in Russian)**.

Dowell SF. Seasonal variation in host susceptibility and cycles of certain infectious diseases. Emerg Infect Dis. 2001;7:369–74.

Downie JC, Hinshaw V, Laver WG. The ecology of influenza isolation of type A influenza viruses from Australian pelagic birds. Aust J Exp Biol Med Sci. 1977;55:635–43.

Erohov SN. White-winged tern. Birds of USSR Laridae. 1988;34:85–97 **(in Russian)**.

Fouchier RA, Munster V, Wallensten A, Bestebroer TM, Herfst S, Smith D, Rimmelzwaan GF, Olsen B, Osterhaus AD. Characterization of a novel influenza A virus hemagglutinin subtype (H16) obtained from black-headed gulls. J Virol. 2005;79:2814–22.

Germundsson A, Madslien KI, Hjortaas MJ, Handeland K, Jonassen CM. Prevalence and subtypes of influenza A viruses in wild waterfowl in Norway 2006–2007. Acta Vet Scand. 2010;52:28.

Gilbert M, Chaitaweesub P, Parakamawongsa T, Premashthira S, Tiensin T, Kalpravidh W, Wagner H, Slingenbergh J. Free-grazing ducks and highly pathogenic avian influenza. Emerg Infect Dis. 2006;12:227–34.

Hoffmann E, Stech J, Guan Y, Webster RG, Perez DR. Universal primer set for the full-length amplification of all influenza A viruses. Arch Virol. 2001;146:2275–89.

Hurt AC, Hansbro PM, Selleck P, Olsen B, Minton C, Hampson AW, Barr IG. Isolation of avian influenza viruses from two different transhemispheric migratory shorebird species in Australia. Arch Virol. 2006;151:2301–9.

Marchenko VYu, Alekseev AYu, Tserennorov D, Yurlov AK, Susloparov IM, Sharshov KA, Ilyinykh FA, Zolotykh SI, Abmed D, Otgonbaatar D, Shestopalov AM. Results of the influenza virus surveillance in wild birds in Western part of Mongolia. Asian Pac J Trop Med. 2010a;2:90–3.

Marchenko VYu, Sharshov KA, Silko NYu, Susloparov IM, Durymanov AG, Zaykovskaya AVu, Alekseev AY, Smolovskaya OV, Stefanenko AP, Malkova EM, Shestopalov AM. Characterization of the H5N1 influenza virus isolated during an outbreak among wild birds in Russia (Tuva Republic) in 2010. Mol Genet Microbiol Virol. 2010b;4:186–90.

Marchenko VY, Alekseev AY, Sharshov KA, Petrov VN, Silko NY, Susloparov IM, Tserennorov D, Otgonbaatar D, Savchenko IA, Shestopalov AM. Ecology of influenza virus in wild bird populations in central Asia. Avian Dis. 2012a;56:234–7.

Marchenko VYu, Sharshov KA, Shestopalov AM. Ecology of influenza virus in wild bird populations in central Asia. Bull East Sib Sci Center Sib Branch Russ Acad Med Sci. 2012b;5:271–5 **(in Russian)**.

Neumann G, Kawaoka Y. Host range restriction and pathogenicity in the context of influenza pandemic. Emerg Infect Dis. 2006;12:881–6.

Rogers SO, Starmer WT, Castello JD. Recycling of pathogenic microbes through survival in ice. Med Hypotheses. 2004;63:773–7.

Sayfutdinova SG, Sharshov KA, Gerasimov YuN, Shestopalov AM. Ecology of influenza A viruses, isolated from gulls of the Russian Far East. Bull East Sib Sci Center Sib Branch Russ Acad Med Sci. 2012;5:316–8 **(in Russian)**.

Sharshov KA, Zolotykh SI, Fedorov EG, Ivanov IV, Druziaka AV, Shestopalov AM, Netesov SV. Surveillance for avian influenza virus in synanthropic birds during epizootic and postepizootic periods on the south of west Siberia. Zh Mikrobiol Epidemiol Immunobiol. 2007;4:53–6.

Sharshov K, Romanovskaya A, Uzhachenko R, Durymanov A, Zaykovskaya A, Kurskaya O, Ilinykh P, Silko N, Kulak M, Alekseev A, Zolotykh S, Shestopalov A, Drozdov I. Genetic and biological characterization of avian influenza H5N1 viruses isolated from wild birds and poultry in Western Siberia. Arch Virol. 2010;155:1145–50.

Sharshov KA, Durymanov AG, Romanovskaya AA, Zaĭkovskaya AV, Marchenko VYu, Silko NYu, Ilinykh FA, Susloparov IM, Alekseev AYu, Shestopalov AM. Molecular-biological and antigenic features of H5N1 subtype highly pathogenic influenza virus strains isolated in southern Siberia in 2005–2009. Zh Mikrobio lEpidemiol Immunobiol. 2011;5:40–3 **(in Russian)**.

Sharshov KA, Marchenko VYu, Yurlov AK, Shestopalov AM. Ecology and evolution of highly pathogenic avian influenza H5N1 in Russia (2005–2012). Bull East Sib Sci Center Sib Branch Russ Acad Med Sci. 2012;5:393–6 **(in Russian)**.

Sharshov K, Sivay M, Liu D, Pantin JM, Marchenko V, Durymanov A, Alekseev A, Damdindorj T, Gao GF, Swayne DE, Shestopalov A. Molecular characterization and phylogenetics of areassortant H13N8 influenza virusisolated from gullsin Mongolia. Virus Genes. 2014a;49:237–49.

Sharshov KA, Sivay MV, Marchenko VYu, Alekseev AYu, Li LX, Shestopalov AM, Shkurupiy VA. Pathogenic potential assessment of avian H13N8 influenza virus, isolated from herring gull (*Larus argentatus*). Bull Novosibirsk State Univ Ser Biol Clin Med. 2014b;2:5–11 **(in Russian)**.

Sivay MV, Silko NV, Sharshov KA, Prokudin AV, Li L, Yang M, Cao S, Shestopalov AM. The role of wild goose (*Anser*) populations of Russia and the Tibet Plateau in the spread of the avian influenza virus. Chin Birds. 2011;2:140–6.

Sivay MV, Sayfutdinova SG, Sharshov KA, Alekseev AY, Yurlov AK, Runstadler J, Shestopalov AM. Surveillance of influenza A virus in wild birds in the Asian portion of Russia in 2008. Avian Dis. 2012a;56:456–63.

Sivay MV, Yurlov AK, Druzyaka AV, Sharshov KA, Shestopalov AM. Rare influenza virus subtypes isolated from birds of the south of Western Siberia. Bull East Sib Sci Center Sib Branch Russ Acad Med Sci. 2012b;5:319–22 **(in Russian)**.

Sivay MV, Baranovich T, Marchenko VY, Sharshov KA, Govorkova EA, Shestopalov AM, Webby RJ. Influenza A (H15N4) virus isolation in Western Siberia, Russia. J Virol. 2013;87:3578–82.

Sivay MV, Sharshov KA, Pantin JM, Muzyka VV, Shestopalov AM. Avian influenza virus with hemagglutinin-neuraminidase combination H8N8, isolated in Russia. Genome Announc. 2014;2:e00545–14.

Stallknecht DE, Shane SM. Host range of avian influenza virus in free-living birds. Vet Res Commun. 1988;12:125–41.

Veen J, Yurlov AK, Delany SN, Mihantiev AI, Selivanova MA, Boere GC. An Atlas of Movements of Southwest Siberian Waterbirds. Wageningen: Wetlands International; 2005.

Webster RG, Bean WJ, Gorman OT, Chambers TM, Kawaoka Y. Evolution and ecology of influenza A viruses. Microbiol Rev. 1992;56:152–79.

Zaykovskaya AV, Saifutdinova SG, Marchenko VYu, Sharshov KA, Durymanov AG, Zolotykh SI, Shmatova LV, Demchin PM, Yushkov YuG, Donchenko AS, Neduzhko VA, Shestopalov AM. Elimination of influenza A virus in mass mortality of wild birds in Krasnoyarsk Territory. Sib Herald Agric Sci. 2011;1:88–93 **(in Russian)**.