
Historical Prevalence and Distribution of Avian Influenza Virus A(H7N9) among Wild Birds

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We examined 48 published studies for which sample sizes could be ascertained to determine the historic prevalence of influenza A(H7N9) virus in wild bird populations and reviewed GenBank data to further establish its distribution. Low prevalence (0.0093%) in Asia suggests > 30,000 samples would be required to detect the H7N9 subtype in wild birds.

Beginning in February 2013, and ongoing at publication of this article, infections with the zoonotic virus, influenza A(H7N9), have caused serious illness in humans in provinces of southeastern China. On April 4, the China Animal Disease Control Centre announced that the virus had been detected in samples collected from a pigeon and chickens at a market in Shanghai (1,2). On April 17, the virus was detected in a sample from a wild pigeon in Nanjing, Jiangsu Province (3). Chen et al. concluded that humans were infected by domestic birds (1); no human-to-human transmission was detected or suspected (4). The structure of the hemagglutinin (HA) protein in the virus and the lack of reports of severe disease in poultry indicate that the virus exhibits characteristics of low pathogenicity in birds (5,6). Recent phylogenetic analysis indicates that the HA segment of the H7N9 subtype is closely related to a strain that was isolated from domestic ducks in Zhejiang, China, in 2011. The neuraminidase (NA) gene of the H7N9 subtype is closely related to that of a strain that was isolated from wild bird samples in South Korea in a location adjacent to a domestic bird production facility; additionally, 6 internal

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genes are closely related to those of an A(H9N2) virus isolated from a brambling (*Fringilla montifringilla*) sample during 2012 in Beijing, China (7,8).

Little information exists on the status of A(H7N9) virus in wild birds to assess their potential as sources of human infection and disseminators of the virus to new areas. Here we report the historic distribution and prevalence of H7N9 subtypes among wild birds preceding this outbreak. This subtype was not known to cause disease in humans until the outbreak during February in China. We also examine the prevalence of individual H7, N9, and H9N2 subtypes in Asia. Finally, we estimate the sample size necessary to detect this low pathogenicity strain of avian influenza virus in wild birds.

The Study

To determine prevalence of H7, N9, H7N9, and H9N2 subtypes, we reviewed 48 peer-reviewed avian influenza surveillance studies in which sample sizes were stated and subtypes were nonselectively detected by using sequence analysis, reverse transcription PCR, or hemagglutination inhibition and neuraminidase inhibition assays. Data from these studies are summarized in the online Technical Appendix (wwwnc.cdc.gov/EID/article/19/12/13-0649-Techapp1.pdf). These included 9 studies conducted in Asia, 12 in Europe, 4 in Africa, 3 in Australia, 17 in North America, and 3 in Latin America. Extended datasets from peer-reviewed studies in Mongolia and Taiwan were provided by M. Gilbert and M.C. Cheng, respectively. The studies sampled birds during 1976–2012.

To further establish the geographic distribution of known H7N9 subtypes, we reviewed GenBank records downloaded on April 26, 2013, for HA or NA segments isolated from birds (9). We included a partially sequenced HA gene (1,676 bp [GenBank accession no. JN244232]) from A/wild bird/Korea/A3/2011 in our comparison (Table) after evaluating the published phylogenetic trees (8).

Apparent prevalence was calculated as the (no. positive samples)/(no. tested) × 100%. The regional estimate for Asia was an unweighted calculation based on the sum of all positive samples and all tested birds, irrespective of detection biases that may have arisen from different wild bird surveillance systems. We determined the minimum sample size to detect at least 1 positive sample based on a 0.05 level of significance (10).

Influenza H7N9 subtypes have been identified among wild birds globally (but not necessarily sequenced or submitted to GenBank) by isolation and by using reverse transcription PCR. The H7N9 subtype has been reported among wild birds from Delaware (USA)/Alberta (Canada), Guatemala, Spain, Sweden, Egypt, Mongolia, and Taiwan (online Technical Appendix Table 1). In these 48 studies, subtype H7N9 has not been detected in wild birds in these locations in Asia: Russia (combined sample size 7,353),

Table. GenBank nucleotide sequences of H7N9 samples, country of origin, hosts, and wild or domesticated status*

HA GenBank accession no.	NA GenBank accession no.	Year	Host (family/genus/species)	Location	Status
KC899669	KC899671	2013	Chicken (<i>Gallus gallus</i>)	China	Domestic
GU060482	GU060484	2009	Goose (Anatidae)	Czech Republic	Domestic
HQ244415	HQ244417	2009	Goose (Anatidae)	Czech Republic	Domestic
CY067670	CY067672	2008	Blue-winged teal (<i>Anas discors</i>)	Guatemala	Wild
CY067678	CY067680	2008	Blue-winged teal (<i>Anas discors</i>)	Guatemala	Wild
AB813056	ND	2011	Mallard (<i>Anas platyrhynchos</i>)	Japan	Unknown
AB481212	AB481213	2008	Wild duck (Anatidae)	Mongolia	Wild
JN244232†	JN244223	2011	Wild bird	South Korea	Wild
ND	JX679164	2008	Wild duck (Anatidae)	South Korea	Wild
HQ244409	HQ244407	2008	Common teal (<i>Anas crecca</i>)	Spain	Wild
AY999981	ND	2002	Mallard (<i>Anas platyrhynchos</i>)	Sweden	Wild
CY024818	CY024820	2006	Blue-winged teal (<i>Anas discors</i>)	USA, Ohio	Wild
JX899805	ND	2011	Goose (Anatidae)	USA, Nebraska	Unknown
JX899803	ND	2011	Guinea fowl (Galliformes)	USA, Nebraska	Domestic
CY133649	CY133651	2011	Northern shoveler (<i>Anas clypeata</i>)	USA, Mississippi	Wild
EU684261	ND	2000	Ruddy turnstone (<i>Arenaria interpres</i>)	USA, Delaware	Wild
CY127253	CY127255	1995	Ruddy turnstone (<i>Arenaria interpres</i>)	USA, Delaware	Wild
CY014786	CY014788	1988	Turkey (<i>Meleagris</i> spp.)	USA, Minnesota	Wild/domestic‡

*HA, hemagglutinin sequence; NA, neuraminidase sequence; ND, no data were available for this variable.

†Partial sequence.

‡Insufficient information was provided to determine status.

Japan (4,335), South Korea (28,214), or China (158) (online Technical Appendix Table 2); furthermore, when subtype H7N9 was detected in Asia, its prevalence was low (online Technical Appendix Table 2).

In countries within Asia, <0.1% of samples from wild birds tested positive for any H7 subtype; <0.05% tested positive for any N9 subtype; <0.01% tested positive for an H7N9 strain, and <0.02% tested positive for an H9N2 strain (online Technical Appendix Table 2). Assuming an apparent prevalence of 0.01%, we estimate that $\geq 30,000$ birds would have to be sampled to detect 1 bird that was H7N9-positive with a 95% probability. To similarly detect 1 bird that was positive for H7, N9, or the H9N2 subtype in Asia, >4,000, 7,000, or 19,000 samples from birds, respectively, would be required.

Since 1988, the HA- and NA-producing genes of avian influenza subtype H7N9 have been deposited in GenBank 12 times, mainly representing isolates collected from wild bird hosts (Table). In Asia, before this outbreak, an H7N9 strain was sequenced from a wild bird in South Korea that was sampled during 2011 in a migratory bird habitat adjacent to duck farms (7) and also during 2011 in a sample from a mallard duck of unknown status from Japan. In 2008, the other H7N9 strain sequences collected in Asia were from a wild duck that was sampled in South Korea and from a wild bird sampled in Mongolia. All virus sequences were obtained from ducks and domestic geese, with the exception of a chicken in China and the following from birds in the United States: a turkey in Minnesota, a guinea fowl in Nebraska, and ruddy turnstones (*Arenaria interpres*) sampled in Delaware during 1995 and 2000. Eight of the complete HA and NA genetic sequences are attributed to wild birds, 3 are attributed to domestic birds, and 1 is attributed to a

bird that could not be identified as wild or domestic because insufficient information was available.

Conclusions

Variation in the methods used in each study makes a precise calculation of H7N9 subtype prevalence in all wild birds impossible to determine, but given the available data, we conclude that the occurrence of the H7N9 subtype in wild bird populations is rare. We also conclude that sample sizes adequate to detect the virus among wild birds will be in the tens of thousands. Publishing the sample size and genus and species of wild birds tested in China will provide a better estimate of the prevalence among these birds related to this outbreak, especially because wild song birds have been hypothesized to be a possible reservoir (11). Wild birds are recorded as the predominant source of H7N9 sequences, but this may be an outcome of sampling bias. Because virologists typically focus on highly pathogenic strains in humans and domestic birds, and an H7N9 subtype was not recognized as highly pathogenic, the H7N9 strains were not tested for as frequently in wild birds. The HA/NA subtype concept we used for this analysis is archaic, omitting the contributions of internal protein genes to the biology of a virus; unfortunately, it is the only widespread typing system available for influenza viruses. Subsequently, the best historic prevalence estimate of the circulating internal genes is based on the H9N2 subtype.

Infection with the H7N9 subtype may prove challenging to control by culling birds, because infected domestic flocks may be asymptomatic. In wild bird populations, low pathogenicity strains are likely to be sustained longer than highly pathogenic strains, which have been unable to persist in wild populations in the absence of introductions

from a domestic reservoir (12). Further research should focus on identifying sequences within the new H7N9 genome that are linked to increased human pathogenicity and transmissibility and on conducting surveillance to detect these markers in viruses carried by both domestic and wild birds (13).

In summary, we present evidence that wild bird surveillance for the novel influenza A(H7N9) virus will require large sample sizes. Given the low likelihood of detection, risk-based surveillance is recommended. Ruling out wild birds as a continuing source of infection for domestic birds or humans will be critical to informing strategies to control the spread of this emerging zoonotic disease.

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References

- Chen Y, Liang W, Yang S, Wu N, Gao H, Sheng J, et al. Human infections with the emerging avian influenza A H7N9 virus from wet market poultry: clinical analysis and characterisation of viral genome. *Lancet*. 2013;6736:1916–25.
- OIE World Animal Health Information Database. Low pathogenic avian influenza (poultry), People's Republic of China, April 4, 2013 [cited 2013 Apr 20]. http://www.oie.int/wahis_2/public/wahid.php/Reviewreport/Review?page_refer=MapFullEventReport&reportid=13225
- ProMED-mail. Avian influenza (38): China, zoonotic LPAI H7N9, wild pigeon, OIE [cited 2013 Apr 17]. <http://www.promedmail.org/archive/no.20130417.1652959>.
- World Health Organization. Global alert and response: human infection with influenza A(H7N9) virus in China—update, 2013 Apr 19 [cited 2013 Apr 19]. http://www.who.int/csr/don/2013_04_19/en/index.html
- Kageyama T, Fujisake S, Takashita E, Xu H, Yamada S, Uchida Y, et al. Genetic analysis of novel avian A(H7N9) influenza viruses isolated from patients in China, February to April 2013. *Euro Surveill*. 2013;18:20453
- World Health Organization. Risk assessment: human infections with influenza A(H7N9) virus, 2013 Apr, 13 [cited 2013 Apr 23]. http://www.who.int/influenza/human_animal_interface/influenza_h7n9/RiskAssessment_H7N9_13Apr13.pdf
- Kim HM, Oh JH, Seo SH. Genetic characterization of avian influenza viruses isolated from waterfowl in southern part of South Korea in 2006. *Virus Genes*. 2008;37:49–51. <http://dx.doi.org/10.1007/s11262-008-0230-4>
- Gao R, Cao B, Hu Y, Feng Z, Wang D, Hu W, et al. Human infection with a novel avian-origin influenza A (H7N9) virus. *N Engl J Med*. 2013;368:1888–97. <http://dx.doi.org/10.1056/NEJMoa1304459>.
- National Center for Biotechnology and Information. Influenza Virus Database [cited 2013 Apr 17]. <http://www.ncbi.nlm.nih.gov/genomes/FLU/Database/nph-select.cgi?go=database>
- Jovanovic BD, Levy PS. A look at the rule of three. *Am Stat*. 1997;51:137–9.
- Arima Y, Zu R, Murhekar M, Vong S, Shimada T. Human infections with avian influenza A(H7N9) virus in China: preliminary assessments of the age and sex distribution. *Western Pac Surveill and Response J*. 2013;4:9–11. <http://dx.doi.org/10.5365/wpsar.2013.4.2.005>
- Gilbert M, Jambal L, Karesh WB, Fine A, Shiilegdamba E, Dulam P, et al. Highly pathogenic avian influenza virus among wild birds in Mongolia *PLoS One*. 2012;7:e44097. <http://dx.plos.org/10.1371/journal.pone.0044097>
- Jonges M, Meijer A, Fouchier RA, Koch G, Li J, Pan JC, et al. Guiding outbreak management by the use of influenza A(H7Nx) virus sequence analysis *Euro Surveill*. 2013;18:20460.

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Historic Prevalence and Distribution of Avian Influenza Virus A(H7N9) among Wild Birds

Technical Appendix

Technical Appendix Table 1. Global distribution and prevalence of influenza H7N9 virus in wild birds

Country/state (reference)	Years sampled	No. tested	No. (%) H7N9	H7N9 virus-positive birds	Population sampled*: no. positive for any avian influenza virus/no. captured (%)
Guatemala (1)	2006–2010	256	1 (0.39)	Blue-winged teal (<i>Anas discors</i>)	Anatidae: 28/234 (12); Picidae: 1/21 (4.8); Tyrannidae: 1/1 (100)
Spain (2)	2005–2007	1,435	2 (0.14)	Mallards (<i>Anas platyrhynchos</i>)	Anseriformes: 29/628 (4.6); Ciconiformes: 3/308 (1); Charadriiformes: 0/217; Gruiformes: 3/180 (1.7); Columbiformes: 0/31; Pelecaniformes: 0/29; Passeriformes: 0/24; Phoenicopteriformes: 2/7 (28.6); Other: 0/11
Spain (3)	2005–2009	1,236	1 (0.081)	Common teal (<i>Anas crecca</i>)	Anatidae: 54/686 (7.9%); Laridae 2/256 (0.8%); Phoenicopteridae: 4/154 (2.5%); Rallidae: 1/80 (1.3%); Ardeidae: 0/12; Porphyridae: 0/12; Porphyridae: 0/12; Columbidae: 0/9; Procellariidae: 0/9; Phalacrocoracidae: 0/6; Scolopacidae: 0/4; Recurvirostridae: 0/2; Sternidae: 0/2; Alcedinidae: 0/1; Fringillidae: 0/1; Phasianidae: 0/1; Stercorariidae: 0/1.
Egypt (4)	2003–2007	6,070	2 (0.033)	Northern shovelers (<i>Anas clypeata</i>)	Anatidae majority: not reported.
Delaware, USA (5)	2000–2005	6,340	2 (0.032)	Mix of shorebirds and ducks	<i>Arenaria interpres</i> : 262/2368 (11%); <i>Calidris canutus</i> : 15/1993 (0.75); <i>Calidris alba</i> : 8/745 (1.1); <i>Calidris alpina</i> : 1/377 (0.26); <i>Calidris pusilla</i> : 4/439 (0.91%); <i>Limnodromus griseus</i> : 1/157 (0.64%); <i>Calidris minutilla</i> : 0/127; <i>Larus atricilla</i> : 1/78 (1.3%); <i>Rynchops niger</i> : 0/49; <i>Larus argentatus</i> : 0/5; <i>Tringa semipalmatus</i> : 0/2
Mongolia (6)	2005–2009	3,950	1 (0.025)	Wild duck, goose, swan or gull	Not reported: <i>Cygnus cygnus</i> ; <i>Anser indicus</i> ; <i>Bucephala clangula</i> ; <i>Tadorna ferruginea</i> ; <i>Anas platyrhynchos</i> ; <i>Anas strepera</i> ; Laridae
Taiwan (7) + this study	1998–2011	44,786	8 (0.018)	Wild ducks	Anatidae 229/20812 (1.1%); Shorebirds 3/6435 (0.05%); Laridae (2/617, 0.32%); Ardeidae (2/825, 0.24%); other birds (1/598, 0.17%)
Delaware, USA, & Alberta, Canada (8)	1976–2001	17,732	2 (0.011)	Mix of shorebirds and ducks	Anatidae (2989/13466, 22.2%); Charadriiformes— <i>Larus atricilla</i> and <i>L. argentatus</i> majority (606/4266, 14.2%)

*Populations sampled represent individual published studies in correlating countries/states.

Technical Appendix Table 2. Influenza H7, N9, H7N9, and H9N2 prevalence in Asia*

Country (reference)	Years monitored	No. tested	No. positive (%)				Population sampled:** no. positive for any avian influenza virus/no. captured (%)
			H7	N9	H7N9	H9N2	
Mongolia (6)	2005–2009	3,950	2 (0.0506)	1 (0.0253)	1 (0.0253)	0	Not reported: <i>Anser indicus</i> ; <i>Anas platyrhynchos</i> ; <i>Anas strepera</i> ; <i>Bucephala clangula</i> ; <i>Cygnus cygnus</i> ; <i>Tadorna ferruginea</i> ; Laridae
Taiwan (7) + this study	1998–2011	44,786	49 (0.109)	23 (0.0514)	8 (0.0179)	0	Anatidae: 229/20812 (1.1); shorebirds: 3/6435 (0.05%); Laridae: 2/617 (0.32%); Ardeidae: 2/825 (0.24%); other birds: 1/598 (0.17%)
Asia (Kazakhstan, Mongolia, & Russia) (9)	2003–2009	2,604	0	0	0	0	Anseriformes: 9/604 (1.5%); Charadriiformes 1/684 (0.14%); Passeriformes: 2/674 (0.30); Ciconiiformes: 0/300; Gruiformes: 0/118; Podicipediformes 1/45 (2.2%); Pelecaniformes: 3/95 (3.2%); Falconiformes: 1/42 (2.4%); Galliformes: 0/16; Columbiformes: 0/18; Coraciiformes: 0/3; Cuculiformes: 0/2; Piciformes: 0/2; Strigiformes: 0/1
Russia (10)	2008	5,678	0	0	0	0	Anatidae: 30/2017 (1.5%); Araeidae: 1/81 (1.2%); Laridae: 10/1,553 (0.64%); Rallidae: 1/164 (0.61); Podicipediformes: 0/64; Scolopacidae: 0/334; Alcidae: 0/19; Charadriidae: 0/190; Recurvirostridae: 0/1; Stercorariidae: 0/1; Columbiformes: 0/25; Passeriformes: 0/989; Galliformes: 0/3; Strigiformes: 0/5; Accipitriformes: 0/8; Coraciiformes: 0/26; Apodiformes: 0/1; Piciformes: 0/3; Guidae: 0/1; Gaviiformes: 0/1; Pelecaniformes: 0/187; Procellariiformes: 0/5
Japan (11)	2001–2008	4,335	0	6 (0.138)	0	1 (0.0231)	Anatidae: 41/4309 (0.95%); Laridae 0/26
South Korea (12)	2003–2008	28,214	13 (0.0461)	7 (0.0248)	0	6 (0.0213)	Anseriformes: 225/28214 (0.8%)
China (13)	2005–2006	158	0	0	0	0	Anatidae: 20/144 (15%); Ardeidae: 0/2; Accipitridae: 0/4; Charadriidae: 0/1; Corvidae: 0/1; Falconidae: 0/2; Guidae: 0/2; Rallidae: 0/1; Phasianidae: 0/1; Upupidae: 0/1
Iran (14)	2003–2007	1,146	2 (0.175)	2 (0.175)	0	9 (0.785)	Podicipedidae: 0/19; Phalacrocoracidae: 0/14; Ardeidae: 0/22; Phoenicopteridae: 0/12; Anatidae: 31/745 (4.2%); Rallidae: 4/234, (1.8%); Recurvirostridae: 0/6; Charadriidae: 0/17; Scolopacidae: 0/51; Laridae: 0/25; Sternidae: 0/1
Mongolia (15) + this study	2009–2012	5,831	6 (0.103)	2 (0.0343)	0	0	Anatidae: (80/5731 (1.4%); Laridae: 0/100
Asia total	1998–2012	96,702	72 (0.0745)	41 (0.0424)	9 (0.0093)	16 (0.0166)	NA†

*Populations sampled represent individual published studies in correlating countries/states.

†NA, not applicable.

References

1. González-Reiche AS, Morales-Betoulle ME, Alvarez D, Betoulle JL, Müller ML, Sosa SM, et al. Influenza A viruses from wild birds in Guatemala belong to the North American lineage. PLoS ONE. 2012;7:e32873. [PubMed http://dx.doi.org/10.1371/journal.pone.0032873](http://dx.doi.org/10.1371/journal.pone.0032873)

2. Pérez-Ramírez E, Gerrikagoitia X, Barral M, Höfle U. Detection of low pathogenic avian influenza viruses in wild birds in Castilla-La Mancha (south central Spain). *Vet Microbiol.* 2010;146:200–8. [PubMed http://dx.doi.org/10.1016/j.vetmic.2010.05.008](http://dx.doi.org/10.1016/j.vetmic.2010.05.008)
3. Busquets N, Alba A, Napp S, Sánchez A, Serrano E, Rivas R, et al. Influenza A virus subtypes in wild birds in North-Eastern Spain (Catalonia). *Virus Res.* 2010;149:10–8. [PubMed http://dx.doi.org/10.1016/j.virusres.2009.12.005](http://dx.doi.org/10.1016/j.virusres.2009.12.005)
4. Soliman A, Saad M, Elassal E, Amir E, Plathonoff C, Bahgat V, et al. Surveillance of avian influenza viruses in migratory birds in Egypt, 2003-09. *J Wildl Dis.* 2012;48:669–75. [PubMed http://dx.doi.org/10.1016/j.jwilddis.2012.05.005](http://dx.doi.org/10.1016/j.jwilddis.2012.05.005)
5. Hanson BA, Luttrell MP, Goekjian VH, Niles L, Swayne DE, Senne DA, et al. Is the occurrence of avian influenza virus in Charadriiformes species and location dependent? *J Wildl Dis.* 2008;44:351–61. [PubMed http://dx.doi.org/10.1016/j.jwilddis.2008.05.005](http://dx.doi.org/10.1016/j.jwilddis.2008.05.005)
6. Tseren-Ochir E-O, Damdinjav B, Sharkhuu T, Kang HM, Sakoda Y, Purevsuren B, et al. Epidemiology of avian influenza viruses in wild birds in Mongolia. *Int J Infect Dis.* 2010;14:e164. <http://dx.doi.org/10.1016/j.ijid.2010.02.1846>.
7. Cheng MC, Lee MS, Ho YH, Chyi WL, Wang CH. Avian influenza monitoring in migrating birds in Taiwan during 1998–2007. *Avian Dis.* 2010;54:109–14. [PubMed http://dx.doi.org/10.1637/8960-061709-Reg.1](http://dx.doi.org/10.1637/8960-061709-Reg.1)
8. Krauss S, Walker D, Pryor SP, Niles L, Chenghong L, Hinshaw VS, et al. Influenza A viruses of migrating wild aquatic birds in North America. *Vector Borne Zoonotic Dis.* 2004;4:177–89. [PubMed http://dx.doi.org/10.1089/vbz.2004.4.177](http://dx.doi.org/10.1089/vbz.2004.4.177)
9. Marchenko VY, Alekseev AY, Sharshov KA, Petrov VN, Silko NY, Susloparov IM, et al. Ecology of influenza virus in wild bird populations in Central Asia. *Avian Dis.* 2012;56:234–7. [PubMed http://dx.doi.org/10.1637/9834-061611-ResNote.1](http://dx.doi.org/10.1637/9834-061611-ResNote.1)
10. Sivay MV, Sayfutdinova SG, Sharshov KA, Alekseev AY, Yurlov AK, Runstadler J, et al. Surveillance of influenza A virus in wild birds in the Asian portion of Russia in 2008. *Avian Dis.* 2012;56:456–63. [PubMed http://dx.doi.org/10.1637/9868-080111-Reg.1](http://dx.doi.org/10.1637/9868-080111-Reg.1)
11. Fujimoto Y, Ito H, Shivakoti S, Nakamori J, Tsunekuni R, Otsuki K, et al. Avian influenza virus and paramyxovirus isolation from migratory waterfowl and shorebirds in San-in district of western Japan from 2001 to 2008. *J Vet Med Sci.* 2010;72:963–7. [PubMed http://dx.doi.org/10.1292/jvms.10-0012](http://dx.doi.org/10.1292/jvms.10-0012)

12. Kang HM, Jeong OM, Kim MC, Kwon JS, Paek MR, Choi JG, et al. Surveillance of avian influenza virus in wild bird fecal samples from South Korea, 2003–2008. *J Wildl Dis.* 2010;46:878–88. [PubMed](#)
13. Zeng X, Hua Y, Li X, Zhang Z. Monitoring influenza A virus and Newcastle disease virus in migratory waterfowls in Sanjiang natural reserve of Heilongjiang Province. *Wei Sheng Wu Xue Bao.* 2008;48:1403–7. [PubMed](#)
14. Fereidouni SR, Werner O, Starick E, Beer M, Harder TC, Aghakhan M, et al. Avian influenza virus monitoring in wintering waterbirds in Iran, 2003–2007. *Virology.* 2010;7:43. [PubMed](#)
<http://dx.doi.org/10.1186/1743-422X-7-43>
15. Gilbert M, Jambal L, Karesh WB, Fine A, Shiilegdamba E, Dulam P, et al. Highly pathogenic avian influenza virus among wild birds in Mongolia. *PLoS ONE.* 2012;7:e44097. [PubMed](#)
<http://dx.doi.org/10.1371/journal.pone.0044097>
16. Pereda AJ, Uhart M, Perez AA, Zaccagnini ME, La Sala L, Decarre J, et al. Avian influenza virus isolated in wild waterfowl in Argentina: evidence of a potentially unique phylogenetic lineage in South America. *Virology.* 2008;378:363–70. [PubMed](#)
<http://dx.doi.org/10.1016/j.virol.2008.06.010>
17. Escudero G, Munster VJ, Bertellotti M, Edelaar P. Perpetuation of avian influenza in the Americas: examining the role of shorebirds in Patagonia. *The Auk.* 2008;125:494–5
<http://dx.doi.org/10.1525/auk.2008.2408.2>
18. Haynes L, Arzey E, Bell C, Buchanan N, Burgess G, Cronan V, et al. Australian surveillance for avian influenza viruses in wild birds between July 2005 and June 2007. *Aust Vet J.* 2009;87:266–72. [PubMed](#) <http://dx.doi.org/10.1111/j.1751-0813.2009.00446.x>
19. Peroulis I, O'Riley K. Detection of avian paramyxoviruses and influenza viruses amongst wild bird populations in Victoria. *Aust Vet J.* 2004;82:79–82. [PubMed](#)
<http://dx.doi.org/10.1111/j.1751-0813.2004.tb14650.x>
20. Mackenzie JS, Edwards EC, Holmes RM, Hinshaw VS. Isolation of ortho- and paramyxoviruses from wild birds in Western Australia, and the characterization of novel influenza A viruses. *Aust J Exp Biol Med Sci.* 1984;62:89–99. [PubMed](#) <http://dx.doi.org/10.1038/icb.1984.9>
21. Munster VJ, Baas C, Lexmond P, Waldenström J, Wallensten A, Fransson T, et al. Spatial, temporal, and species variation in prevalence of influenza A viruses in wild migratory birds. *PLoS Pathog.* 2007;3:e61. [PubMed](#) <http://dx.doi.org/10.1371/journal.ppat.0030061>

22. Gaidet N, Dodman T, Caron A, Balanca G, Desvaux S, Goutard F, et al. (2007) Influenza surveillance in wild birds in Eastern Europe, the Middle East, and Africa: preliminary results from an ongoing FAO-led survey. *J Wildl Dis.* 2007;43: Suppl : S22–8.
http://www.jwildlifedis.org/content/43/3_Supplement/S22.full
23. Lebarbenchon C, Chang CM, van der Werf S, Aubin JT, Kayser Y, Ballesteros M, et al. Influenza A virus in birds during spring migration in the Camargue, France. *J Wildl Dis.* 2007;43:789–93.
[PubMed](#)
24. Hlinak A, Mühle RU, Werner O, Globig A, Starick E, Schirrmeier H, et al. A virological survey in migrating waders and other waterfowl in one of the most important resting sites of Germany. *J Vet Med B Infect Dis Vet Public Health.* 2006;53:105–10. [PubMed](#)
<http://dx.doi.org/10.1111/j.1439-0450.2006.00935.x>
25. Süss J, Schäfer J, Sinnecker H, Webster RG. Influenza virus subtypes in aquatic birds of eastern Germany. *Arch Virol.* 1994;135:101–14. [PubMed](#) <http://dx.doi.org/10.1007/BF01309768>
26. De Marco MA, Foni E, Campitelli L, Delogu M, Raffini E, Chiapponi C, et al. Influenza virus circulation in wild aquatic birds in Italy during H5N2 and H7N1 poultry epidemic periods (1998 to 2000). *Avian Pathol.* 2005;34:480–5. [PubMed](#) <http://dx.doi.org/10.1080/03079450500368185>
27. Terregino C, De Nardi R, Guberti V, Scremin M, Raffini E, Martin AM, et al. Active surveillance for avian influenza viruses in wild birds and backyard flocks in Northern Italy during 2004 to 2006. *Avian Pathol.* 2007;36:337–44. [PubMed](#) <http://dx.doi.org/10.1080/03079450701488345>
28. Henriques AM, Fagulha T, Barros SC, Ramos F, Duarte M, Luís T, et al. Multiyear surveillance of influenza A virus in wild birds in Portugal. *Avian Pathol.* 2011;40:597–602. [PubMed](#)
<http://dx.doi.org/10.1080/03079457.2011.618943>
29. Tolf C, Bengtsson D, Rodrigues D, Latorre-Margalef N, Wille M, Figueiredo ME, et al. Birds and viruses at a crossroad—surveillance of influenza A virus in Portuguese waterfowl. *PLoS ONE.* 2012;7:e49002. [PubMed](#) <http://dx.doi.org/10.1371/journal.pone.0049002>
30. Cumming GS, Caron A, Abolnik C, Cattoli G, Bruinzeel LW, Burger CE, et al. The ecology of influenza A viruses in wild birds in southern Africa. *EcoHealth.* 2011;8:4–13. [PubMed](#)
<http://dx.doi.org/10.1007/s10393-011-0684-z>
31. Baumer A, Feldmann J, Renzullo S, Müller M, Thür B, Hofmann MA. Epidemiology of avian influenza virus in wild birds in Switzerland between 2006 and 2009. *Avian Dis.* 2010;54:875–84.
[PubMed](#) <http://dx.doi.org/10.1637/9119-110209-Reg.1>

32. Kulak MV, Ilinykh FA, Zaykovskaya AV, Epanchinzeva AV, Evstaphiev IL, Tovtunec NN, et al. Surveillance and identification of influenza A viruses in wild aquatic birds in the Crimea, Ukraine (2006–2008). *Avian Dis.* 2010;54:1086–90. [PubMed http://dx.doi.org/10.1637/9272-020510-ResNote.1](http://dx.doi.org/10.1637/9272-020510-ResNote.1)
33. Simulundu E, Ishii A, Igarashi M, Mweene AS, Suzuki Y, Hang'ombe BM, et al. Characterization of influenza A viruses isolated from wild waterfowl in Zambia. *J Gen Virol.* 2011;92:1416–27. [PubMed](#)
34. Hinshaw VS, Wood JM, Webster RG, Deibel R, Turner B. Circulation of influenza viruses and paramyxoviruses in waterfowl originating from two different areas of North America. *Bull World Health Organ.* 1985;63:711–9. [PubMed](#)
35. Krauss S, Pryor SP, Raven G, Danner A, Kayali G, Webby RJ, et al. Respiratory tract versus cloacal sampling of migratory ducks for influenza A viruses: are both ends relevant? *Influenza Other Respi Viruses.* 2013;7:93–6. [PubMed http://dx.doi.org/10.1111/j.1750-2659.2012.00359.x](http://dx.doi.org/10.1111/j.1750-2659.2012.00359.x)
36. Wille M, Robertson GJ, Whitney H, Ojkic D, Lang AS. Reassortment of American and Eurasian genes in an influenza A virus isolated from a great black-backed gull (*Larus marinus*), a species demonstrated to move between these regions. *Arch Virol.* 2011;156:107–15. [PubMed http://dx.doi.org/10.1007/s00705-010-0839-1](http://dx.doi.org/10.1007/s00705-010-0839-1)
37. Ito T, Okazaki K, Kawaoka Y, Takada A, Webster RG, Kida H. Perpetuation of influenza A viruses in Alaskan waterfowl reservoirs. *Arch Virol.* 1995;140:1163–72. [PubMed http://dx.doi.org/10.1007/BF01322743](http://dx.doi.org/10.1007/BF01322743)
38. Ramey AM, Pearce JM, Flint PL, Ip HS, Derksen DV, Franson JC, et al. Intercontinental reassortment and genomic variation of low pathogenic avian influenza viruses isolated from northern pintails (*Anas acuta*) in Alaska: examining the evidence through space and time. *Virology.* 2010;401:179–89. [PubMed http://dx.doi.org/10.1016/j.virol.2010.02.006](http://dx.doi.org/10.1016/j.virol.2010.02.006)
39. Koehler AV, Pearce JM, Flint PL, Franson JC, Ip HS. Genetic evidence of intercontinental movement of avian influenza in a migratory bird: the northern pintail (*Anas acuta*). *Mol Ecol.* 2008;17:4754–62. [PubMed http://dx.doi.org/10.1111/j.1365-294X.2008.03953.x](http://dx.doi.org/10.1111/j.1365-294X.2008.03953.x)
40. Ramey AM, Pearce JM, Reeves AB, Franson JC, Petersen MR, Ip HS. Evidence for limited exchange of avian influenza viruses between seabirds and dabbling ducks at Alaska Peninsula coastal lagoons. *Arch Virol.* 2011;156:1813–21. [PubMed http://dx.doi.org/10.1007/s00705-011-1059-z](http://dx.doi.org/10.1007/s00705-011-1059-z)

41. Siembieda JL, Johnson CK, Cardona C, Anchell N, Dao N, Reisen W, et al. Influenza A viruses in wild birds of the Pacific flyway, 2005–2008. *Vector Borne Zoonotic Dis.* 2010;10:793–800. [PubMed http://dx.doi.org/10.1089/vbz.2009.0095](http://dx.doi.org/10.1089/vbz.2009.0095)
42. Stallknecht DE, Shane SM, Zwank PJ, Senne DA, Kearney MT. Avian influenza viruses from migratory and resident ducks of coastal Louisiana. *Avian Dis.* 1990;34:398–405. [PubMed http://dx.doi.org/10.2307/1591427](http://dx.doi.org/10.2307/1591427)
43. Wilcox BR, Knutsen GA, Berdeen J, Goekjian V, Poulson R, Goyal S, et al. Influenza-A viruses in ducks in northwestern Minnesota: fine scale spatial and temporal variation in prevalence and subtype diversity. *PLoS ONE.* 2011;6:e24010. [PubMed http://dx.doi.org/10.1371/journal.pone.0024010](http://dx.doi.org/10.1371/journal.pone.0024010)
44. Lebarbenchon C, Sreevatsan S, Ramakrishnan MA, Poulson R, Goekjian V, Di Matteo JJ, et al. Influenza A viruses in American White Pelican (*Pelecanus erythrorhynchos*). *J Wildl Dis.* 2010;46:1284–9. [PubMed http://dx.doi.org/10.2307/1591309](http://dx.doi.org/10.2307/1591309)
45. Krauss S, Walker D, Pryor SP, Niles L, Chenghong L, Hinshaw VS, et al. Influenza A viruses of migrating wild aquatic birds in North America. *Vector Borne Zoonotic Dis.* 2004;4:177–89. [PubMed http://dx.doi.org/10.1089/vbz.2004.4.177](http://dx.doi.org/10.1089/vbz.2004.4.177)
46. Slemons RD, Shieldcastle MC, Heyman LD, Bednarik KE, Senne DA. Type A influenza viruses in waterfowl in Ohio and implications for domestic turkeys. *Avian Dis.* 1991;35:165–73. [PubMed http://dx.doi.org/10.2307/1591309](http://dx.doi.org/10.2307/1591309)
47. Alfonso CP, Cowen BS, van Campen H. Influenza A viruses isolated from waterfowl in two wildlife management areas of Pennsylvania. *J Wildl Dis.* 1995;31:179–85. [PubMed http://dx.doi.org/10.2307/1591309](http://dx.doi.org/10.2307/1591309)
48. Hanson BA, Swayne DE, Senne DA, Lobpries DS, Hurst J, Stallknecht DE. Avian influenza viruses and paramyxoviruses in wintering and resident ducks in Texas. *J Wildl Dis.* 2005;41:624–8. [PubMed http://www.jwildlifedis.org/content/41/3/624.long](http://www.jwildlifedis.org/content/41/3/624.long)