



The avian and mammalian host range of highly pathogenic avian H5N1 influenza



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ABSTRACT

Highly pathogenic H5N1 influenza viruses have been isolated from a number of avian and mammalian species. Despite intensive control measures the number of human and animal cases continues to increase. A more complete understanding of susceptible species and of contributing environmental and molecular factors is crucial if we are to slow the rate of new cases. H5N1 is currently endemic in domestic poultry in only a handful of countries with sporadic and unpredictable spread to other countries. Close contact of terrestrial bird or mammalian species with infected poultry/waterfowl or their biological products is the major route for interspecies transmission. Intra-species transmission of H5N1 in mammals, including humans, has taken place on a limited scale though it remains to be seen if this will change; recent laboratory studies suggest that it is indeed possible. Here we review the avian and mammalian species that are naturally susceptible to H5N1 infection and the molecular factors associated with its expanded host range.

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1. Introduction

Influenza A viruses belong to the family *Orthomyxoviridae* with the majority of viruses maintained in wild aquatic bird reservoirs, predominantly those of the anseriform species. Classification of these viruses is determined by the two surface glycoproteins, the hemagglutinin (HA) and neuraminidase (NA) of which 16 HA and 9 NA subtypes have been isolated from aquatic birds (Kim et al., 2009). The migratory nature of the aquatic fowl reservoir results in the wide geographic spread and distribution of most circulating subtypes. A consequence of this geographic distribution in migratory birds is the potential contact of infected bird with domestic avian and mammalian species, including humans, with novel influenza A subtypes that can cross the host range barrier and initiate local epidemics or widespread influenza pandemics (Webster et al., 1992).

Since their detection in Asia in 1996, the highly pathogenic avian influenza (HPAI) H5N1 viruses have spread to many countries in the eastern hemisphere becoming endemic in populations of domestic birds in a more restricted number of countries and transiently infecting a number of other hosts along the way. The mechanism of virus spread throughout the hemisphere is not entirely clear, but probably as a result of both wild birds and poultry trade. While wild

and domestic species may have contributed to spread, it is at the level of the domestic waterfowl and poultry interface that many mammalian species, humans included, are likely at the highest risk of acquiring H5N1 infection (Fig. 1). Because of the high potential for H5N1 to negatively impact veterinary and human health and subsequently the global economy, understanding the host range of the virus is of utmost importance. This review will focus on detailing the avian species susceptible to infection with HPAI H5N1 influenza viruses and the factors (and species) that influence the onward transmission to mammalian hosts (Fig. 2).

Influenza viruses encoding HA of subtype H5 and paired with varying NA subtypes are maintained as low pathogenic avian influenza (LPAI) forms in many anseriform species (Sharp et al., 1997, 1993; Süss et al., 1994). In 1996 the antecedent HPAI H5N1 virus A/Goose/Guangdong/1/96 was detected on a goose farm in Southern China causing an outbreak in the summer and early fall with 40% morbidity in birds (Xu et al., 1999). Reassortants of this virus were next detected in domestic poultry, ducks, and geese in Hong Kong in 1997 (Shortridge et al., 1998) with associated human cases resulting from direct contact with infected birds {Claas:1998jy}. Genetic analysis of all 8 gene segments from the 1997 viruses revealed substantial homology to other concomitantly circulating avian influenza viruses; with the internal genes being donated by either A/Quail/Hong Kong/G1/1997 (H9N2) or A/Teal/Hong Kong/W312/1997 (H6N1) viruses of domestic poultry (Guan et al., 1999; Hoffmann et al., 2000). While the 1997 outbreak was controlled following depopulation, H5N1 viruses continued to circulate in the wider region in at least ducks and geese

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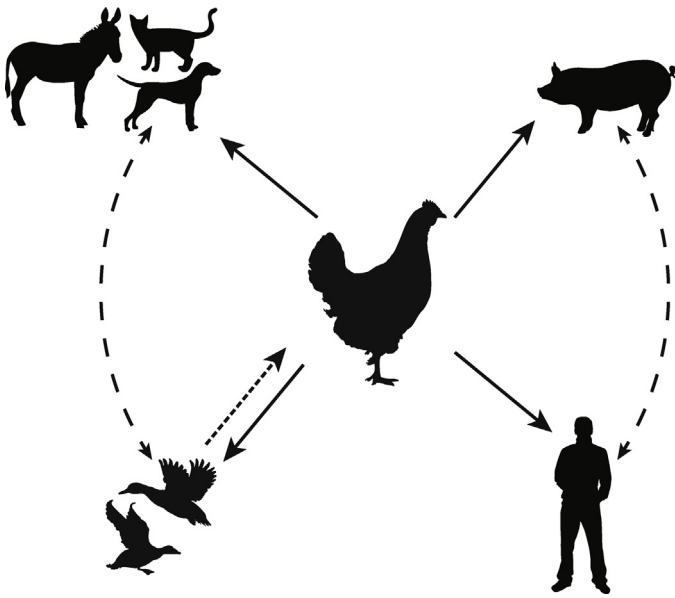


Fig. 1. Routes of H5N1 species distribution. H5N1 influenza viruses cross the species barrier through close contact with infected birds, in particular domestic poultry. Contact with domestic poultry (chickens, ducks, etc.) has resulted in the inter-species transmission of H5N1 to non-avian hosts. Infrequently documented is the transmission of H5N1 from wild migratory birds to domestic and/or captive mammals. Though not documented, swine to human transmission of influenza subtypes H1N1, H2N2, and H3N2 does occur in nature.

(Guan et al., 2002a) generating a number of reassortants. While the reassortment partners of the H5N1 viruses were considered to be viruses of aquatic bird origin, there was no evidence of infection of wild birds with the highly pathogenic virus. This changed in 2002 when H5N1 viruses were detected in resident waterfowl and flamingos as well as wild little egrets and gray herons and other wild migratory birds; of particular note was the fact that the infection was lethal in some of the aquatic birds, an atypical presentation in these hosts {Sturm-Ramirez:2004dq}. While it is unclear what hosts were critical in maintaining the virus during the intervening time, 2004 saw the emergence of H5N1 in an extended number of countries {Li:2004ez}. While the details of this geographic expansion and associated genetic diversification are detailed elsewhere in this publication, it was associated with an expansion of hosts in which the virus has been found.

2. H5N1 influenza in wild bird species

All influenza virus subtypes circulate in wild bird populations taxonomically classified in the orders Anseriformes and Charadriiformes; the order Anseriformes is composed of aquatic species (ducks, geese, swans) whereas shore birds (gulls, sandpipers, surf-birds, terns) are grouped into order Charadriiformes. Though many avian species are susceptible to infection with H5N1 influenza viruses, it is the anseriform species that have been implicated in their global spread (Kim et al., 2009). While it is generally accepted that transition to the highly pathogenic form of influenza virus occurs in gallinaceous poultry species and the majority of prior

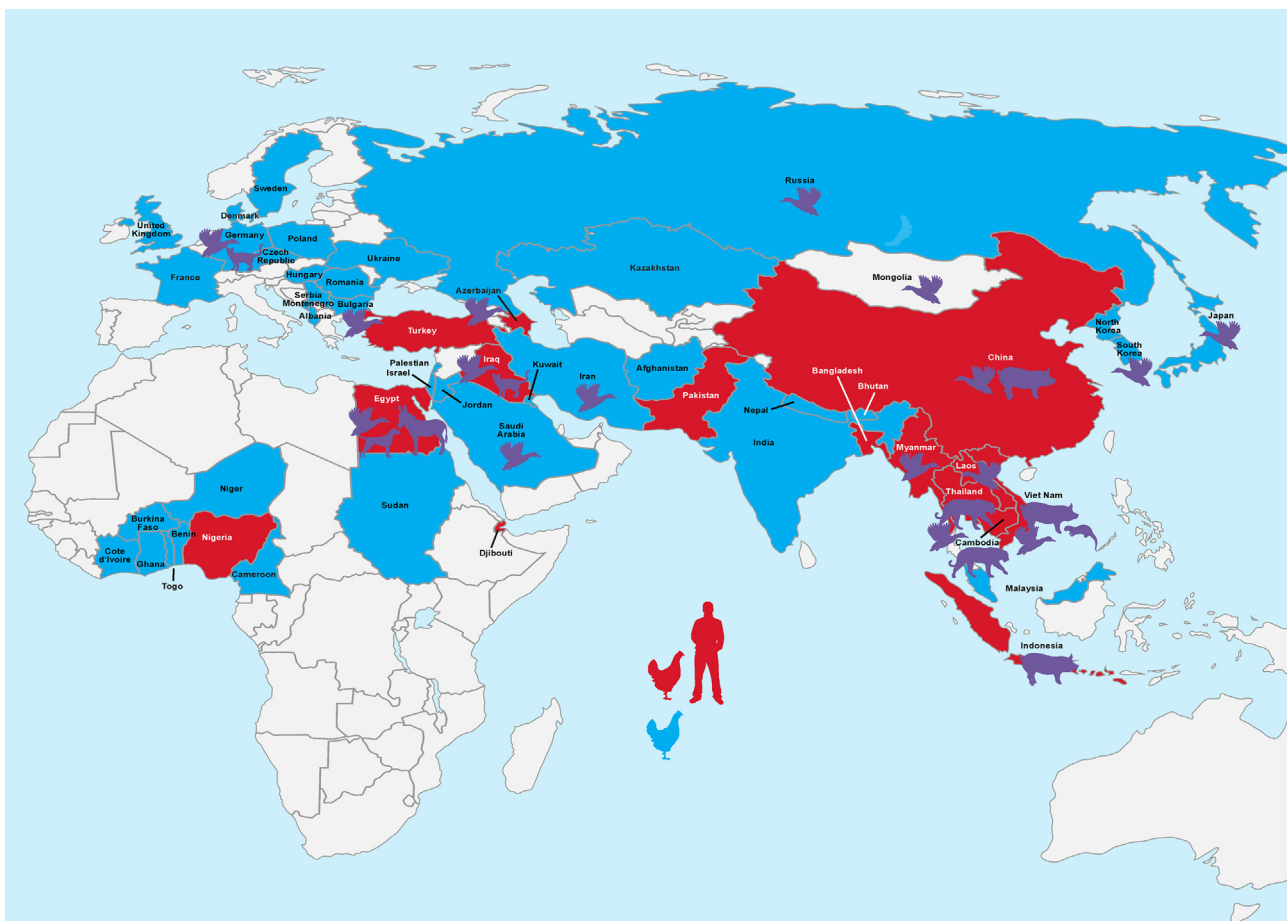


Fig. 2. Global distribution of H5N1 infection. Countries shaded in red have concurrent H5N1 outbreak in domestic poultry and humans. Blue countries signify outbreaks only in wild avian species. Additional cases of mammalian H5N1 are depicted as shaded figures (<http://www.fao.org/avianflu>, http://www.oie.int/wahis_2/public/wahid.php/Diseaseinformation/Diseasedistributionmap, http://www.who.int/influenza/human_animal_interface/EN_GIP_20120810CumulaCumulativeN5N1cases.pdf).

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