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REVIEW ARTICLE

Avian influenza: Eco-epidemiological aspects of the virus in its natural hosts, the migratory waterfowls

Influenza aviar: Aspectos ecoepidemiológicos del virus en su hospedero natural, las aves acuáticas migratorias

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ABSTRACT

Avian influenza viruses produce mainly respiratory and intestinal diseases. Their relevance in the generation of pandemic strains has led to a large amount of research to understand their distribution in nature, as well as the relations that become established for the effective transmission among different hosts. Waterfowl have been recognized as their natural reservoir and they play an important role in the propagation and generation of the diversity of these viruses. The emergence of new influenza viruses with pandemic potential among the human population (H5N1 of avian origin or recombinant H1N1 with avian segments) point our lack of information on many aspects of the ecology and epidemiology of these viruses in their natural hosts to enable the implementation of more effective prevention and control measures. In this review, we attempt to make a critical essay on the current state of knowledge on the biotic and abiotic factors that influence the ecology and epidemiology of the influenza A viruses in wild birds.

Key words: avian influenza, ecology, epidemiology, migratory birds.

RESUMEN

Los virus influenza ocasionan enfermedades respiratorias e intestinales. Su importancia en la generación de cepas pandémicas ha conducido a la realización de intensa investigación científica para entender y conocer su distribución en la naturaleza, así como las relaciones que se establecen para la transmisión efectiva entre diferentes hospederos. Las aves acuáticas principalmente del orden Anseriformes, se han reconocido como el reservorio de estos virus y tienen una participación crucial en la propagación y generación de diversidad de estos virus. La emergencia de nuevos virus influenza con potencial pandémico entre la población humana (H5N1 de origen aviar y el actual virus pandémico H1N1 que presenta segmentos aviarios), resalta la falta de información sobre muchos aspectos de la ecología y epidemiología de estos virus en sus hospederos naturales, que permitan la implementación de medidas más efectivas de prevención y control. En esta contribución revisamos el estado del arte del conocimiento sobre los factores bióticos y abióticos que influyen en la ecología y epidemiología de los virus influenza en aves silvestres.

Palabras clave: aves migratorias, ecología, epidemiología, influenza aviar.

INTRODUCTION

Influenza is an acute respiratory disease that has affected the human species along history. The episode known as Spanish influenza (subtype H1N1), which occurred in 1918, is among the most remembered catastrophic pandemic event, because it caused approximately 50 million deaths in the world population (Belshe 2005). In the last century, diverse disease outbreaks caused by H1N1, H2N2, H3N2 subtypes have occurred, all with

a high mortality case rate (millions of deaths) (Oxford 2000). In the mid of 1997, a new influenza subtype known as highly pathogenic H5N1 appeared in Asia, this virus affected initially domestic fowl; however, human cases were also recorded (Yuen et al. 1998, Tran et al. 2004, Beigel et al. 2005). Due to its infection and dispersion characteristics, this virus can potentially unchain a pandemic outbreak of influenza. Since 2003, this virus has infected more than 499 people in 15 countries of Asia, Africa, and the Middle East, with a 59 % case

fatality rate (WHO 2010). A detailed description of the human cases geographic dispersion since 2003 is depicted in Table 1.

An important barrier that limits the dispersion of these viruses to new hosts has been the recognition of sialic acid receptors in the membrane of the infected cells. Hemagglutinin is the main antigen of the viral surface; in the viruses of avian origin, it binds preferentially to receptors with the α SA2-6Gal β , whereas the human viruses bind to receptors α SA2-3Gal β , (Suzuki 2005). The transmission of viruses from infected domestic fowl to humans has occurred in a poorly efficient manner, and the transmission from human to human has been even less efficient (Vong et al. 2006). The latter has been explained based on findings on the tropism of the H5N1 virus by human cells of the lower airways (type II pneumocytes and alveolar macrophages) (van Riel et al. 2006, 2007). This is believed to contribute to the pulmonary lesion and limits physically the effective dispersion of the virus through the respiratory particles from the diseased individual to the environment.

TABLE 1

Cumulative number of confirmed human cases of avian influenza A/H5N1 reported to WHO during 2003-2010.

Número de casos humanos confirmados de influenza aviar A/H5N1 reportados a la OMS, y acumulados durante 2003-2010.

Country	Cases	Deaths
Azerbaijan	8	5
Bangladesh	1	0
Cambodia	10	8
China	39	26
Djibouti	1	0
Egypt	109	34
Indonesia	165	136
Irak	3	2
Lao People's Democratic Republic	2	2
Myanmar	1	0
Nigeria	1	1
Pakistan	3	1
Thailand	25	17
Turkey	12	4
Viet nam	119	59
Total	499	295

ECOLOGY OF THE INFLUENZA A VIRUS

Role of aquatic and terrestrial birds

During more than three decades, diverse reports have supported the hypothesis that the natural reservoir of the influenza viruses are the aquatic birds, particularly the migratory ones, and that this plays an important role in their biology and propagation (Alexander 2000). The bird orders in which these viruses present more often are the Anseriformes (ducks, geese, and swans) and the Charadriiformes (shore birds, seagulls). In an extensive literature review performed by (Stallknecht & Shane 1988), the presence of these viruses is reported in 12 orders (Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Galliformes, Gruiformes, Columbiformes, Charadriiformes, Piciformes, and Passeriformes) and in 88 species of wild birds (aquatic and terrestrial). Recently, (Olsen et al. 2006) published list with more than 90 species, representing 25 families and 13 orders (Table 2), we updated this information including the new Latin-American registries. It is possible that, due to the interest that has arisen for the influenza viruses in the last years, important information will be described on these and other species included in the surveillance programs in many regions of the world. Although viruses have been isolated from terrestrial species, their proportion with respect to aquatic fowl is small, hence their role in the preservation and ecology of the influenza A viruses has been considered to be limited (Kaleta 2003). However, it is not possible to affirm from the available reports, that their participation is nil in maintaining some subtypes, because these species have been poorly studied.

Biotic factors

According to the transmission cycle of influenza A viruses and their maintenance among populations of waterfowl, it has been suggested that the latter might be determined by biotic and abiotic factors, although the mechanisms have not been elucidated yet. Among the biotic factors are those related to the reproductive and gregarious behavior of

many species and to the migration phenomenon. The migration process is a common strategy of birds to occupy seasonal habitats, and can go from local movements to intercontinental migrations (Olsen et al. 2006). Wild ducks migrate to satisfy diverse vital biological needs. Migration takes them to the South at the end of the summer and autumn in search of better climates, and they return to the North to their reproduction areas at the

end of the winter or the start of the spring (Delogu et al. 2003). During the pre-migration period, the individuals in reproductive age gather in large numbers in the mating and nursing grounds, where birds of different ages get in contact. This phenomenon favors the fast transmission of the virus among immunologically immature individuals or more susceptible ones, such as juveniles (Hinshaw et al. 1980).

TABLE 2

Detection of Avian influenza virus in different taxa worldwide (adapted from supplementary material, Olsen et al. 2006), new Latin American registries are shown with reference.

Detección de virus influenza aviar en diferentes taxa en el mundo (adaptado del material complementario de Olsen et al. 2006), los nuevos registros de Latinoamérica se muestran con la referencia.

Common name	Species	Location
Anseriformes, Anatidae		
American black duck	<i>Anas rubripes</i>	Canada, USA (Pennsylvania, New York, Maryland)
American wigeon	<i>Anas americana</i>	Canada (Toronto), USA (Pennsylvania, Ohio), México (Sonora)* (Montalvo-Corral & Hernández 2010)
Australian shelduck	<i>Tadorna tadornoides</i>	Australia
Blue-winged teal	<i>Anas discors</i>	Canada, USA (Ohio, NY, Oklahoma)
Bufflehead	<i>Bucephala albeola</i>	Canada, USA (Ohio)
Cakling goose	<i>Branta hutchinsi</i>	USA (Pacific Coast) (Dusel et al. 2009)
Canada goose	<i>Branta canadensis</i>	Canada, USA (Minnesota, Delaware, Ohio, Maryland, NY, Pennsylvania)
Canvasback	<i>Aythya valisineria</i>	Canada
Cinnamon teal	<i>Anas cyanoptera</i>	USA, Perú, México (Cuevas-Domínguez 2009)
	<i>Anas cyanoptera orinmus</i>	Bolivia (Spackman et al. 2007)
Common shelduck	<i>Tadorna tadorna</i>	Italy
Common teal	<i>Anas crecca</i>	Japan, France, East Germany, Iceland, The Netherlands, Canada, USA (Ohio, Oklahoma, Louisiana), Mexico (Sonora)* (Montalvo-Corral & Hernández 2010)
Egyptian goose	<i>Alopochen aegyptiacus</i>	South Africa
Eurasian wigeon	<i>Anas penelope</i>	Japan, France, Italy, The Netherlands
Falcated teal	<i>Anas falcata</i>	Japan, USSR
Gadwall	<i>Anas strepera</i>	The Netherlands, Canada, USA (Arkansas, Ohio, Louisiana)
Garganey	<i>Anas querquedula</i>	Romania (Stallknecht et al. 1988)
Greater white-fronted	<i>Anser albifrons</i>	Japan, Netherlands, USA
Green-winged teal	<i>Anas carolinensis</i>	Canada, USA (Ohio, Pennsylvania, Oklahoma)
Greylag goose	<i>Anser anser</i>	East Germany
Hooded merganser	<i>Lophodytes cucullatus</i>	Canada (Parmley 2008)
Long-tailed duck	<i>Clangula hyemalis</i>	East Germany
Mallard	<i>Anas platyrhynchos</i>	Israel, Japan, New Zealand, Austria, Czechoslovakia, France, East Germany, Hungary, Italy, The Netherlands, Sweden, Canada, USA
Mottled duck	<i>Anas fulvivula</i>	USA (Louisiana)
Mute swan	<i>Cignus olor</i>	East Germany, USA
Northern pintail	<i>Anas acuta</i>	Israel, Japan, France, Italy, The Netherlands, Canada, USA
Northern shoveler	<i>Anas clypeata</i>	Canada, Japan, USA, México* (Montalvo-Corral & Hernández 2010)
Pacific black duck	<i>Anas superciliosa</i>	Australia

Table 2. (Continued)

Common name	Species	Location
Redhead	<i>Aythya americana</i>	Canada, USA, México* (Montalvo-Corral & Hernández 2010)
Ring-necked duck	<i>Aythya collaris</i>	Canada, USA
Ruddy duck	<i>Oxyura jamaicensis</i>	Canada, USA
South african shelduck	<i>Tadorna cana</i>	South Africa
Spot-billed duck	<i>Anas poecilorhyncha</i>	Japan
Sunda teal	<i>Anas gibberifrons</i>	Australia
Tufted duck	<i>Aythya fuligula</i>	Japan, Italy
Tundra swan	<i>Cygnus columbianus</i>	Japan, USA, Northern Europe
Wandering whistling-duck	<i>Cynus columbianus</i>	Japan, Northern Europe, USA
White-cheeked pintail	<i>Anas bahamensis</i>	Peru (Gherzi et al. 2009)
White winged scoter	<i>Melanitta fusca</i>	East Germany
Whooper swan	<i>Cignus cignus</i>	Japan
Wood duck	<i>Aix sponsa</i>	USA, Canada
Yellow-billed duck	<i>Anas undulata</i>	South Africa
Charadriiformes, Charadriidae		
Shorebirds	spp.	USA, East Germany
Charadriiformes, Haematopodidae		
American oystercatcher	<i>Haematopus palliatus</i>	Peru (Gherzi et al. 2009)
Charadriiformes, Laridae		
Arctic tern	<i>Sterna paradisaea</i>	USSR
Black noddy	<i>Anous minutus</i>	Australia
Black-headed gull	<i>Larus ridibundus</i>	East Germany, Australia, The Netherlands, Sweden
Black-tailed gull	<i>Larus crassirostris</i>	Japan
Common tern	<i>Sterna hirundo</i>	USSR, East Germany, USA
Franklins gull	<i>Larus pipixcan</i>	USA
Great black-backed gull	<i>Larus marinus</i>	USA
Herring gull	<i>Larus argentatus</i>	USA (Delmarva peninsula, New Jersey)
Kelp gull	<i>Larus dominicanus</i>	Argentina (Pereda et al. 2008), Peru (Gherzi et al. 2009)
Laughing gull	<i>Larus atricilla</i>	USA (New Jersey, Delaware)
Lesser noddy	<i>Anous tenuirostris</i>	Australia
Ring-billed gull	<i>Larus delawarensis</i>	USA
Sandwich tern	<i>Sterna sandvicensis</i>	East Germany
Slender-billed gull	<i>Larus genei</i>	USSR (Stallknecht 1988)
Sooty tern	<i>Sterna fuscata</i>	Australia
White-winged tern	<i>Chlidonias leucopterus</i>	USSR (Stallknecht 1988)
Charadriiformes, Scolopacidae		
Dunlin	<i>Calidris alpina</i>	Japan, USA
Eurasian woodcock	<i>Scolopax rusticola</i>	USSR
Ruddy turnstone	<i>Arenaria interpres</i>	USA, Peru (Gherzi et al. 2009)
Sanderling	<i>Calidris alba</i>	USA
Spur-winged lapwing	<i>Vanellus spinosus</i>	India
Temminck's stint	<i>Calidris temminckii</i>	USSR
Whimbrel	<i>Numenius phaeopus</i>	Peru (Gherzi et al. 2009)
Ciconiiformes, Ardeidae		
Grey heron	<i>Ardea cinerea</i>	USSR, Romania
Squacco heron	<i>Ardeola ralloides</i>	Romania
Ciconiiformes, Threskiornithidae		
Glossy ibis	<i>Plegadis falcinellus</i>	Romania
Hadada ibis	<i>Bostrychia hagedash</i>	South Africa
Columbiformes, Columbidae		
Eurasian collared dove	<i>Sreptopelia decaocto</i>	Hungary
Galliformes, Phasianidae		
Common pheasant	<i>Phasianus colchicus</i>	Hungary, Italy, USA
Rock partridge	<i>Alectoris graeca</i>	Israel
Gaviiformes, Gaviidae		
Arctic loon	<i>Gavia arctica</i>	Romania
Red-throated loon	<i>Gavia stellata</i>	USSR

Table 2. (Continued)

Common name	Species	Location
Gruiformes, Alcidae		
Common murre	<i>Uria aalge</i>	Russia, Sweden
Gruiformes, Rallidae		
American coot	<i>Fulica americana</i>	Canada, USA
Common moorhen	<i>Gallinula chloropus</i>	Hungary (Stallknecht 1988)
Eurasian coot	<i>Fulica atra</i>	Israel, Australia, East Germany, Hungary, Italy, Sweden
Passeriformes, Emberizidae		
American redstart	<i>Setophaga ruticilla</i>	Canada
Black-faced bunting	<i>Emberiza spodocephala</i>	USSR, Japan
Dark-eyed junco	<i>Junco hyemalis</i>	Canada
Magnolia warbler	<i>Dendroica magnolia</i>	Canada
Song sparrow	<i>Melospiza melodia</i>	Canada
Tennessee warbler	<i>Vermivora peregrina</i>	Canada
Yellow warbler	<i>Dendroica petechia</i>	Canada
Yellow-breasted bunting	<i>Emberiza aureola</i>	USSR
Yellow-throated warbler	<i>Dendroica dominica</i>	Canada
Passeriformes, Fringillidae		
Purple finch	<i>Carpodacus purpureus</i>	Canada
Passeriformes, Hirundinidae		
Barn swallow	<i>Hirundo rustica</i>	Egypt
Passeriformes, Laniidae		
Red-backed shrike	<i>Lanius collurio</i>	Egypt
Yellow wagtail	<i>Motacilla flava</i>	Egypt
Passeriformes, Muscicapidae		
Common redstart	<i>Phoenicurus phoenicurus</i>	Egypt
Hermit thrush	<i>Catharus guttatus</i>	Canada
Nightingale sp.	<i>Luscinia spp</i>	Egypt
Spotted flycatcher	<i>Muscicapa striata</i>	USSR
Passeriformes, Passeridae		
House sparrow	<i>Passer domesticus</i>	Hungary
Passeriformes, Pycnonotidae		
Yellow-vented bulbul	<i>Pycnonotus goiavier</i>	Malaysia
Passeriformes, Sturnidae		
Common starling	<i>Sturnus vulgaris</i>	Israel
Passeriformes, Sylviidae		
Common whitethroat	<i>Sylvia communis</i>	Egypt
Garden warbler	<i>Sylvia borin</i>	Egypt
Icterine warbler	<i>Hippolais icterina</i>	Egypt
Willow warbler	<i>Phylloscopus trochilus</i>	Egypt
Passeriformes, Tyrannidae		
Willow flycatcher	<i>Empidonax traillii</i>	Canada
Pelicaniformes, Pelecanidae		
Peruvian pelican	<i>Pelecanus occidentalis thagus</i>	Peru (Ghera et al. 2009)
Pelicaniformes, Phalacrocoracidae		
Great cormorant	<i>Phalacrocorax carbo</i>	East Germany, Romania
Piciformes, Picidae		
Great-spotted woodpecker	<i>Dendrocopos major</i>	USSR
Podicepsiformes, Podicipedidae		
Pied-billed grebe	<i>Podilymbus podiceps</i>	Canada
Procellariiformes, Procellariidae		
Wedge-tailed shearwater	<i>Puffinus pacificus</i>	Australia
Raptors		
Various		Italy
Tinamiformes, Tinamidae		
Red-winged tinamou	<i>Rhynchotus rufescens</i>	Argentina (Alvarez et al. 2010)
Yellow warbler	<i>Dendroica petechia</i>	Canada

The structure of the populations (proportion of adult and juvenile individuals) among the different species, their routes and migration patterns have been mentioned as factors intervening in the distribution of influenza A viruses. An example of this phenomenon are the Blue-winged teals (*Anas discors*) that start migration earlier, limiting the contact with large communities in the northern hemisphere, and remaining as a susceptible population to become infected in the wintering sites, as has been documented in studies performed in North America (Hanson et al. 2005). The nature and progression of the infection defines also the amount of viral particles excreted to the environment, which has been estimated to last up to 30 days, at concentrations of 10^8 copies of viral RNA/gram of feces, being the transmission route direct fecal-oral through contaminated waters (Hinshaw et al. 1980, Webster et al. 1992).

Influenza A viruses are recognized as pathogens of aquatic birds that have co-evolved along their history and that have established a perfect parasite-host relationship, in which birds are almost asymptomatic to the infection. In wild waterfowl, influenza viruses generally replicate in the cells of the ciliated epithelium of the gastrointestinal tract, which differs from mammals in which infection is manifested in the cells of the non-ciliated epithelium of the respiratory tract (Kida et al. 1980, Ibricevic et al. 2006). In this virus-host relationship, water plays a very important role, since many investigations suggest that the lakes and other lagoon water bodies serve as a long-term abiotic reservoir that enables the preservation of influenza A viruses from one migration cycle to the other, and even for many years (Ito et al. 1995, Zhang et al. 2006, Lang et al. 2008). When these water bodies freeze during the winter they enable the maintenance in their whole state of the viral particles deposited in the fecal material from the infected waterfowl. During defrosting and return of the birds to their reproduction sites, the virus can start the infection cycle when finding new potential hosts.

Abiotic factors

The permanence of these viruses in different water bodies, from fresh to saline waters, is

given by the physicochemical characteristics of the environment and the nature of the strain. At least 25 strains of avian influenza virus of different subtypes have been assessed in studies with a research model system (in distilled water). These studies demonstrated that the persistence of the avian influenza virus (AIV) is inversely proportional to the salinity, pH, and temperature values (Stallknecht et al. 1990a, Brown et al. 2007, Brown et al. 2009). In natural intervals or conditions of these environmental parameters, it has been observed the infectivity of the virus can be preserved for months at 4 °C, a slightly alkaline pH, and a salinity of 0 ppm (Brown et al. 2009). The combined evaluation of the studied physicochemical factors suggests that there is variability in the virus stability in different aquatic habitats. This variability has been observed even among strains of the same subtype, particularly in LPAI H5 and HPAI H5N1 viruses (Brown et al. 2007).

Environmental transmission

Until recently environmental transmission had been neglected or thought it has little relevance in avian influenza epidemiology (Faust et al. 2009). However novel epidemiological models have shed some light in the role of this transmission in sustaining epidemics in waterfowl mainly in small communities (Brebán et al. 2009, Rohani et al. 2009). Between biotic factors involved in the presence of avian influenza virus in aquatic ecosystems, a new topic has emerged. Some authors have reported that invertebrate species inhabiting aquatic environments, in particular bivalves, can influence the persistence and viral loads of AI in water. Filter-feeding bivalves could negatively affect AI virus transmission within aquatic bird populations decreasing available virus in suspension, able to infect birds through consumption of water (Faust et al. 2009).

Little information is available on the molecular mechanisms that participate in the permanence of these viruses in the environment and their infectivity, although involvement of modifications at the structural level of key protein sites, such as in hemagglutinin or in the enzymatic activity of neuraminidase, has been suggested.

EPIDEMIOLOGY OF THE INFLUENZA A VIRUS

Four decades of intense research

After defining the role played by migratory water birds in the ecology of the virus, an intense scientific activity was stimulated to know the distribution of the virus in the wild population. This enabled to set the bases for the current knowledge on the epidemiology of influenza A virus in wild birds in North America, which in turn have been supported by short-term and longitudinal studies performed in different regions of Alaska, Canada, and the USA. The first studies performed in water birds in Canada revealed some aspects on the transmission of these viruses among the wild populations, as well as the high prevalence in juvenile individuals, of up to 60 % at the reproduction sites (Hinshaw et al. 1980, Hinshaw et al. 2003). Other studies have described a diminution in the virus prevalence as the birds migrate to their wintering or resting places in the south of the USA, of 0.25 % (Krauss et al. 2004). Most of the epidemiological studies performed in North America focus on the Central and Mississippi migratory flyway, the Mid-West and South of the USA (Minnesota, Mississippi, Michigan, Pennsylvania, Louisiana, and Texas (Smitka & Maassab 1981, Stallknecht et al. 1990b, Bahl et al., 1975, Alfonso et al. 1995, Hanson et al. 2003) a few studies have focused on the Atlantic (Rosenberger et al. 1974, Deibel et al. 1985) and Pacific flyways (Slemons et al. 1974, Runstadler et al. 2007, Siembieda et al. 2008). The patterns in occurrence of influenzavirus in western hemisphere are very similar to that observed in the eastern hemisphere.

Patterns in the distribution of virus influenza

The presence of the influenza A virus in aquatic birds, as well as in other susceptible populations, depicts a seasonal behavior. The epidemic peaks of influenza in wild birds (mainly in Anseriformes) are observed in the autumn, just before starting migration (Halvorson et al. 1985). However there are differences among groups, it has been observed, in North American populations that, in the order Charadriiformes, the peak or

increase in influenza A virus prevalence occurs in the spring, when the populations return to their reproduction sites. These differences among taxa could suggest another preservation mechanism of some subtypes that are maintained by this group, which allows for the re-introduction of the virus in the next migration season.

When dealing with the influenza virus epidemiology, it is important to point out that a large amount of the available information has been obtained from the study of some avian species that appear recurrently in the published works. Avian influenza viruses have been isolated from 20 of the 42 species of ducks, geese, and swans native of North America, and from 47 species to the 158 known worldwide (Stallknecht & Shane 1988, Olsen et al. 2006). The genus *Anas* spp. has been widely studied, and it is known that some species, mainly dabbling ducks, are more susceptible to the infection.

Anas platyrhynchos or Mallard is one of the species in which the highest prevalence of the influenza A viruses of the different subtypes (up to 23 in juveniles) has been found (Hinshaw et al. 1980). A controversy exists on whether this susceptibility is due to biological factors or is biased by the abundance of this species in the continent and its frequent inclusion in the monitoring studies. Other commonly studied species are *Anas acuta*, *Anas crecca*, *Anas discors*, *Anas clypeata*, *Anas rubripes*, and *Anas americana*. The least studied species are diving ducks (*Aythya* spp., *Melanitta* spp., etc), geese, and swans (*Branta* spp., *Chen* spp., etc), shore birds, and seagulls. From the latter ones, the most complete study known to this date is with birds of this order performed in Delaware Bay, USA, which analyzed 9402 birds of five families: Haematopodidae, Recurvirostridae, Charadriidae, Scolopacidae, and Laridae; including 34 species. Results showed positive birds only in the Scolopacidae (3.3 %) and Laridae (0.6 %) families, and a greater prevalence of positive individuals was observed in the *Arenaria interpres* species (Hanson et al. 2008). The participation of this order in the epidemiology of the influenza viruses is not clear, due to the low prevalence found in the performed studies or its nil presence (Munster et al. 2007).

All known influenza subtypes have been found in wild birds, although in variable proportions. It is assumed that there is a certain degree of specificity for species that carry or maintain only some influenza subtypes among the aquatic birds (Sharp et al. 1993). The most prevalent subtypes or the most frequently found in ducks have been H1, H3, H4, H6, H11, and the least frequent ones are H5, H7, H8, and H9 (Stallknecht et al. 1990b, Hanson et al. 2005, Stallknecht & Brown 2007). Subtypes H14, H15, and H16 have been isolated from Charadriiformes in Europe, (Fouchier et al. 2005) and recently H16 has been identified in the USA from environmental samples, which are assumed to come from shore birds, although in one of the collecting sites the probability of coming from ducks cannot be discarded (VanDalen et al. 2008). The presence of the diverse subtypes varies annually, there are subtypes that are isolated for several years from the same site, and others that disappear (or diminish their frequency and are not detected) and then reappear in subsequent years. The circulation of different subtypes among aquatic bird populations favors the genetic reassortment process through the co-infection with two viral species in the same host. This gives rise to hybrid viruses with different characteristics from the parental ones, increasing the genetic diversity of the influenza viruses. Several studies have identified co-infection processes. Sharp et al. (1997) found that there are HA and NA combinations that are more frequently associated to co-infection (H1N3, H1N9, H2N5, H4N1, H4N4, H6N3, H12N4, and H13N6). These authors suggest that viruses (subtypes) establish in specific hosts, which by being in equilibrium with the bird's immune system prevent the infection by other viruses. Whereas, those viruses that are apparently "less adapted" are more susceptible to establish co-infections. The bird species that apparently are less susceptible to co-infections are *Anas platyrynchos* and *Anas acuta*, this is probably due to their frequent contact with viral species and to the immunity acquired against them.

In the epidemiology of influenza, the virus-host-environment triad must be considered with all its implications. The structure of the population is an important factor, as there is

evidence that the age is a variable that influences the prevalence of the virus. Some studies have attempted to establish in the same way the effect of sex; however, the observations have not been conclusive. In a study performed in Alaska, found a higher prevalence in males (Ip et al. 2008), whereas other authors observed that viruses in females were more prevalent (Runstadler et al. 2007). Other studies have not found differences between sexes (Alfonso et al. 1995, Munster et al. 2007, Wallensten et al. 2007). It is not known if the differences found in some studies have a biological significance, and if there is, indeed, an actual effect of the sex on the predisposition of an individual to acquire the infection, and if this has implications in performance, as some type of physiological alteration.

The prevalence of these viruses in birds is influenced by geographical, seasonal, and demographic factors. It has been hypothesized that resident aquatic birds could play a role in the local persistence of some subtypes (Slemons et al. 2003), however, in a phylogeographic analysis of the viral genomes published in public databases, found evidence that the viruses cluster according to season and locality (Chen & Holmes 2009). These authors have observed the persistence of viral genotypes for one or two years, which strongly suggests that the circulation of influenza strains in the resting sites is mainly due to frequent re-introductions by migratory populations. Some subtypes, considered rare in the past, have been found with higher frequencies due to the increased capture and monitoring efforts in the continent, as is the case of the H5 subtype (Hanson et al. 2003, Munster et al. 2005, Dusek et al. 2009). In addition, the prevalence data in diverse regions of the USA have modified old hypotheses on the occurrence of influenza viruses in the wintering sites. Unusual prevalence has been found in the costal wetlands of the Gulf of Texas (6-15 %) (Hanson et al. 2005, Ferro et al. 2008). Other studies performed in Alaska described prevalence of 0.06 to 25 % (Runstadler et al. 2007, Winker et al. 2007, Ip et al. 2008). These differences have been explained in function of the dates of sampling, the analyzed species, and even the preservation of the samples, and the detection methods.

OCCURRENCE OF INFLUENZA A VIRUS IN LATIN AMERICA

Influenza viruses' prevalence is not well studied in the southern hemisphere. There are some sero-epidemiological studies performed in cormorants and penguins of Ecuador, seashore birds and giant petrels of Argentina, evidencing the exposure of these birds to the virus, but no viral isolations were performed in the assessed species (Uhart et al. 2003, Travis et al. 2006a, 2006b, D'Amico et al. 2007). In an avian influenza outbreak in commercial poultry farms in Chile, in 2002, it was concluded that it was caused by influenza A virus subtype H7N3 (Suarez et al. 2004). Later on, an ancestor was identified from a resident bird of Bolivia (*Anas cyanoptera orinmou*s) collected in 2001. This virus presented five segments very related to the virus from Chile (PB1, PB2, PBA, HA, and NP), two North American segments (NA and M), and one segment related to the South American equine lineage (NS) (Spackman et al. 2006, 2007).

Recently, two monitoring studies were published from South America, which included a large number of species and they might be the first studies performed in this part of the continent providing data on the prevalence of the influenza virus in wild populations. A study conducted in Argentina, sampled 2895 birds of diverse families of the Charadriiformes and Anseriformes orders, finding a 0.41 % prevalence (through RRT-PCR) (Pereda et al. 2008). The only viral isolate obtained from cloacal samples was identified as an H13N9 virus in a species of resident seagulls (*Larus dominicanus*). The ulterior genetic characterization revealed interesting data on a possible new South American lineage evolving independently from the North American. A recent study also conducted in Argentina report the isolation of one influenzavirus H1N1 subtype from a terrestrial non migratory bird, with a genetic configuration supporting the postulated southern hemisphere lineage for internal genes (Alvarez et al. 2010). This renewed the interest in knowing more about the viruses circulating in other regions of America, Africa and Eurasia, where scarce studies have been performed in birds.

Gherzi et al. (2009) evaluated the occurrence of influenza A virus in wetlands of

the central part of Peru, analyzed 2405 samples from 27 species, and they obtained 9 isolates (0.37 %), similarly to the report by Pereda et al. (2008). Four hemagglutinin subtypes (H3, H4, H10, and H13) and four neuraminidases (N2, N5, N8, and N9) were identified in the following combinations, H3N8, H4N5, H10N9, H13N2. Subtype H13N2 was isolated from a seagull (*Larus dominicanus*). Some resident species were found positive; however, it was not possible to assess the persistence of the viruses in the environment during the non-migratory period. The occurrence of an H4N3 virus was identified in the Caribbean in an Anatide species, being this first report for the area (Douglas et al. 2007).

In Mexico, avian influenza reports have been circumscribed to surveillance activities performed by sanitary officials in the poultry farms of the country as part of the permanent campaigns to prevent influenza outbreaks. In 1994, a high pathogenicity influenza outbreak occurred caused by the H5N2 virus, which is still circulating in some regions of the country in its low pathogenicity form (Villareal-Chavez & Flores 2003). It has been suggested that a possible precursor of this virus might have been the low H5N2 pathogenicity virus that had been circulating in the poultry farms and which probably originated from wild birds (Horimoto et al. 1995).

Some studies in wild populations of the coastal wetlands of Sonora have been performed recently as part of the Pacific migratory flyway, finding a 3.6 % occurrence of influenza A virus in different species, such as *Anas americana*, *Anas clypeata*, *Anas crecca*, and *Aythya americana*, the positive samples were identified by conventional PCR and sequencing of the hemagglutinin gene: two H5 viruses, one H6, and one H9 of low pathogenicity of North American lineage (Montalvo-Corral & Hernandez 2010). In addition, in the center of the country, the presence of the H7N3 virus was reported, isolated from a cinnamon teal (*Anas cyanoptera*), in the Estado de Mexico (Cuevas-Domínguez et al. 2009). These reports are the first evidence on the distribution and presence of influenza A virus in migratory populations in the country. There are no arguments to assume that these viruses were not present in the birds wintering in different wetlands of

Mexico and other regions of America, because the aquatic ecosystems richness of the country, along its coasts and interior water bodies, represents unending resting sites, where millions of migratory birds arrive each year and constitute a shared continental resource.

AVIAN INFLUENZA (H5N1)

Migratory birds as potential carriers of highly pathogenic avian influenza virus (H5N1)

The role played by birds as potential vectors of highly pathogenic viruses or perhaps pandemic ones around the world is a debate topic among the scientific community. Some believe that a faster dispersion route is through contaminated poultry material from farm to farm, and the illegal birds traffic from the affected sites to other regions, as was the case of the Thai hawks introduced into Belgium, carriers of H5N1 (van Borm et al. 2005, Rappole & Hubalek 2006). However, considering the fast genetic changes presented by this virus in just a couple of years, it can be considered that its range of dispersion and adaptation to wild species could also increase. Likewise, the potential of many species to act as asymptomatic carriers of the virus, capable of transporting it long distances, has also been described.

The migration patterns are known and there are overlapping zones in some of the intercontinental flyways, as is the case of the Australian-Asiatic migration flyway that interconnects at the Behring strait with the Pacific flyway in America. This is considered a potential input route to the continent of the H5N1 virus, because of the transmission of the virus from Australian-Asiatic species to birds in North America. This transmission phenomenon, although sporadic, from Eurasian viruses to North American birds is known to exist (Marakova et al. 1999).

Avian influenza H5N1 pathology in wild birds

The influenza viruses' paradigm in their natural hosts is that these act as asymptomatic carriers. The first disease case caused by the subtype H5N3 described in

wild populations appeared in South Africa in 1961, and no other report existed (Becker, 1967). This changed in 2002, when it was found that wild birds were also affected by the H5N1 virus. Diverse H5N1 strains have been identified in flocks of aquatic and terrestrial dead birds and in apparently healthy birds in Asia, Europe, and Africa (Ellis et al. 2004, Bragstad et al. 2007, Chen et al. 2006, Ducatez et al. 2007). The pathogenicity of these viruses has been variable in domestic and wild waterfowl, as well as in some terrestrial species. There is evidence of neurological damage, efficient replication in the trachea, and greater tissular tropism in some bird species (ducks and terrestrial birds) that have been experimentally infected with H5N1 HPAI strains (Perkins & Swayne 2003, Sturm-Ramirez et al. 2004, Sturm-Ramirez et al. 2005). However, some non-pathogenic isolates replicate and transmit efficiently, suggesting that H5N1 HPAI strains that cause little damage in ducks, can propagate silently to domestic and wild waterfowl in Asia and the rest of the world (Kou et al. 2005, Keawcharoen et al. 2008).

Zoonotic and pandemic risk of avian influenza viruses

These findings enable us to assume that these zoonotic H5N1 viruses are adapting to new hosts through the fast genetic changes that have occurred in the last six years, and with it they have increased their dispersion to other environments. Although, attention has been focused on the epidemic caused by this virus in Asia and other continents, there are other avian viruses that also need strict surveillance, such as subtypes H9N2 and H7N7, which have also infected humans. Currently, the A/H1N1v (2009) virus that is circulating worldwide as a pandemic virus has genetic characteristics (segments of the viral genome) of viruses infecting swines as well as of those infecting birds. The aforementioned, suggests that the reassortment or genetic rearrangement mechanisms in intermediary hosts could have originated in domestic fowl (turkeys), swines, or even humans, a process that must have been given along several steps and for some time (months or years) (Dawood et al. 2009, Smith et al. 2009).

CONCLUSIONS AND FURTHER REMARKS

The nature of the influenza A viruses in wild bird population is a complex issue that has to be approached from diverse perspectives. The presence and distribution of these viruses in their natural reservoirs and in other hosts are determined by individual, environmental, and, even, social and economic factors. The study of these viruses represent a titanic effort, knowing the diversity of hosts, the inherent viral variability, and all the geographical and seasonal factors that have to be taken into consideration. It has been proposed to use, as a study model, systems or local compartments that would enable understanding the dynamics of the viruses in determined environments and their relations with susceptible hosts in the surroundings of the system or compartments being studied. This strategy, in a local sense, could be used to fill the information loopholes on the prevalence of the viruses in sites where they have not been detected before, to establish temporality and persistence factors in the environment, as well as the flow of genetic material to resident avian hosts, or to other domestic animals.

Another relevant aspect is to entail the different disciplines involved in this issue to the field of virology. It is necessary to consider the knowledge generated in the realm of ornithology and ecology of the different avian species to ascertain the influence exerted by the diverse biological aspects, such as reproduction and migration processes, on the distribution of these viruses. Another barely studied subject is the immunological response of the wild birds to the virus and how the virus can affect their vital processes; this could be approached through follow-up procedures or through field telemetry. The variations in prevalence encountered in diverse studied regions are very wide, as well as the different methodologies used for the detection of the viruses. The classical epidemiological studies have used sero-prevalence assessments, using as gold standard the viral isolation and inhibition of hemagglutination or ELISA to identify the subtypes. With the development of molecular techniques and the increasing number of research on influenza viruses in migratory birds, the most recent reports have been using classical virology techniques

together with molecular biology tools, such as PCR, in either conventional or quantitative ways. The use of these tools has increased the database of known viral genomes in wild birds, which has allowed for the integration of meta-analyses to know the genetic structure of these viruses along many years of gathering viral sequences. Aspects on the dynamics of flow of the different genotypes throughout geographical regions and among different avian host species are beginning to be elucidated. The integrated vision of epidemiology, ecology, and evolution of these viruses will allow to have better tools to predict their occurrence and flow dynamics and of the intra- and inter-species genetic changes. In addition, this knowledge will give rise to better prevention and control programs for these zoonotic or pandemic outbreaks.

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