WILD BIRDS AND THE EPIDEMIOLOGY OF AVIAN INFLUENZA

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ABSTRACT: Although wild birds are the recognized source and reservoir for all subtypes of avian influenza viruses (AIV), the complex interaction among these diverse host and virus populations has not received adequate attention. A general concept of AIV epidemiology in wild birds exists; however, the presence of highly pathogenic avian influenza (HPAI) H5N1 viruses in wild birds has reinforced the need for a much more detailed understanding of AIV natural history. Worldwide, the wild avian reservoirs for AIV are incompletely defined, even within well-studied groups such as the Anseriformes and Charadriiformes. This lack of clarity applies not only to avian host species, but also to the various subtypes of AIV present within these populations. Even with the extensive number of AIV isolations previously reported from wild birds, the reservoir species and global distribution for many of these AIV subtypes are not completely understood. To date, studies related to AIV epidemiology in wild birds primarily focused on the agent. To move forward, we need to apply this same level of scrutiny and detailed understanding to the natural host populations and the environments they utilize. Research to date clearly demonstrates that species and population structure are important in AIV maintenance, transmission, and possibly long-distance movement. Species-related differences related to general behavior, spatial and temporal distribution, habitat utilization, migration behavior, population age structure, and individual species susceptibility all potentially influence a species’ role in AIV epidemiology. The unprecedented mortality associated with HPAI H5N1 infection in wild birds provides a new window from which to view the potential for exchange of AIV between wild and domestic birds, and further demonstrates and expands the varied roles that wild birds may play in AIV epidemiology. These roles must be clearly defined if we are going understand the full implications of current HPAI H5N1 virus introduction into the wild bird populations and most importantly prevent the next one.

Key words: Avian influenza, ducks, epidemiology, HPAI H5N1, natural history, reservoir, wild birds.

Although wild birds are the recognized source and reservoir for all subtypes of avian influenza viruses (AIV) (Hinshaw et al., 1980; Suss et al., 1994), the complex interactions among these diverse host and virus populations has not received adequate attention. A general concept of AIV epidemiology in wild birds exists; however, the presence of highly pathogenic avian influenza (HPAI) H5N1 viruses in wild birds reinforces the need for a much more detailed understanding of AIV natural history. Worldwide, the wild avian reservoirs for AIV are incompletely defined, even within well-studied groups such as the Anseriformes and Charadriiformes. This lack of clarity not only applies to avian host species, but also to the various subtypes of AIV present within these populations. Even with the extensive number of AIV isolation previously reported from wild birds, the reservoir species and global distribution for many of the AIV subtypes are not completely understood. To date, studies related to AIV epidemiology in wild birds primarily focused on the agent. To move forward, we need to apply this same level of scrutiny and detailed understanding to the natural host populations and the environments they utilize.

Like most diseases, the epidemiology of AIV in wild birds is defined by interactions between the host, agent, and environment. This simple concept has important implications not only to understanding the epidemiology of wild-type AIV but also to understanding potential impacts associated with the introduction of HPAI viruses into wild bird populations.
The host and host populations

Naturally occurring infections of AIV are reported from free-living birds representing more than 90 species in 13 avian orders (Stallknecht and Shane, 1988; Olsen et al., 2006). Most of the species are associated with aquatic habitats and two avian orders, the Anseriformes (ducks, geese, and swans) and the Charadriiformes (gulls, terns, and shorebirds). Species within the family Anatidae of the order Anseriformes (specifically ducks, subfamily Anatinae) have accounted for most of the reported AIV isolations; the viruses are reported from 47 (Olsen et al., 2006) of the 158 species of ducks and geese worldwide. More isolations of AIV have been reported from mallards (*Anas platyrhynchos*) than any other species. Within the Chardriiformes, AIVs were isolated from species in three families (Scolopacidae, Laridae, and Alcidae). Within the Scolopacidae, most reported AIV isolations are from one species, the ruddy turnstone (*Arenaria interprets*) (Stallknecht, 1998). Isolations also are reported from seven additional avian orders, which include species commonly associated with aquatic habitats (Ciconiiformes, Gaviiformes, Pelecaniformes, Podicipediformes, and Procellariiformes), but collectively these include only 10 species from which AIV were isolated. Although there are reports of AIV from species in the orders Columbiformes, Piciformes, and Passeriformes, most AIV isolation attempts involving species not associated with aquatic habitats were unsuccessful (Hinshaw and Webster, 1982; Deibel et al., 1985; Nettles et al., 1985); these groups currently are not considered as important AIV reservoirs.

Among migratory birds AIV prevalence can vary greatly according to season and location, and because individual species (and populations within species) exhibit different migratory behaviors, habitat preferences, and geographic ranges, individual species within these reservoir groups may play distinct but important roles in the epidemiology of AIV. As a general model, AIV prevalence in ducks peaks in late summer and early fall. This is associated with premigration staging (Hinshaw et al., 1985) and is clearly the pattern seen in mallards in North America. The pattern is attributed to increased concentrations of susceptible hatching-year birds, leading to AIV infection rates that exceed 30% in juveniles at this time. However, in blue-winged teal (*Anas discors*), an earlier and more long-distance migrant, a more complex pattern emerges. High prevalence rates are recorded when teal are associated with mallards on northern staging areas, but these birds represent only a portion of the continental population of teal. In August and September, very large numbers of blue-winged teal have already left the staging areas and have arrived on wintering areas. Prevalence rate in this portion of the teal population is substantially lower (approximately 8% of these birds are infected in September) (Stallknecht et al., 1990a). These same birds eventually migrate further to wintering areas in both Central and South America and may provide a link for the exchange of AIVs between continents. This scenario suggests that blue-winged teal, by escaping the force of infection in northern staging areas, may represent an important species in the maintenance of AIV through the winter migration period, as evidenced by isolation of AIVs from this species prior to leaving the wintering grounds for spring migration (Hanson et al., 2005). These are just two of many duck species, and it is very possible that individual species contribute differently to the AIV transmission and maintenance cycles. Although ducks are a very well-studied group with regards to the epidemiology of AIV, there are many species and populations worldwide for which little information is available.

The temporal patterns observed in ducks correspond to consistent spatial patterns. In general, AIV prevalence in
North America is highest in waterfowl staging areas in Canada and the northern United States (Hinshaw et al., 1985). During migration, prevalence rapidly decreases, and on wintering areas AIV prevalence often is lower than 1–2% (Stallknecht and Shane, 1988). Low AIV prevalence estimates also occur during winter in ducks in Europe (Fouchier et al., 2003).

Spatial and temporal patterns in Charadriiformes are more difficult to understand. A consistent spatial relationship is observed with ruddy turnstones during spring migration stopovers at Delaware Bay (Kawaoka et al., 1988; Hanson, 2002; Krauss et al., 2004); however, this is the only site, worldwide, where consistent AIV isolations from shorebirds have been reported. In most cases, reported prevalence rates from these species are either very low or negative (Stallknecht, 1998; Hanson, 2002; Fouchier et al., 2003). The epidemiology of AIV in this group of birds is far from understood and as with ducks there are many species for which no information is available.

The viruses

Avian influenza virus subtypes are not equally represented among wild bird populations. This variation can occur between hosts, locations, and years. Most of the AIVs isolated from ducks are represented by viruses in the H3, H4, and H6 subtypes (Stallknecht et al., 1990a; Krauss et al., 2004). The H11 subtype also is common in duck populations (Ottis and Bachman, 1983; Stallknecht et al., 1990a; Slemons et al., 1991). Viruses representing the H5, H7, and H9 generally are reported at low prevalence rates from ducks (Stallknecht and Shane, 1988; Krauss et al., 2004); but these virus subtypes can be more common at specific locations and times (Hanson et al., 2003; Munster et al., 2005). The H8 subtype is extremely rare in ducks with less than 10 isolations reported during the last 20 years in North America (Stallknecht et al., 1990a; Krauss et al., 2004; Hanson et al., 2005). Subtype diversity is not constant between years; predominant subtypes, such as the H3, H4, and H6, are reported to follow a 2-yr cycle, whereas others occur sporadically (Krauss et al., 2004).

In shorebirds and gulls, AIV subtype diversity is not well understood, but differences exist between Charadriiformes species as compared to ducks (Kawaoka et al., 1988; Hanson, 2002; Krauss et al., 2004). To date, nine subtypes of AIVs occur more often in shorebirds than ducks including the H5, H7, H9, and H13 (Krauss et al., 2004). It is important to understand that existing data on subtype diversity in shorebirds are limited in scope with most isolates recovered from one species (ruddy turnstone) at one location (Delaware Bay, USA).

The environment

The transmission and maintenance of AIV in wild bird populations is dependent on fecal/oral transmission (Hinshaw et al., 1979; Sandu and Hinshaw, 1981; Sinnecker et al., 1983). Replication of AIV in ducks occurs primarily in the intestinal tract (Slemons and Easterday, 1975) with high concentrations of infectious virus shed in feces (Webster et al., 1978; Hinshaw et al., 1980). Avian influenza viruses have been isolated from surface water in Alberta, Canada (Hinshaw et al., 1980), Minnesota, USA (Halvorson et al., 1983), and Alaska, USA (Ito et al., 1995).

Despite the recognized importance of fecal/oral transmission of these viruses in wild bird populations, existing data on AIV persistence in water are extremely limited. The potential for environmental persistence of these viruses was reported initially by Webster et al. (1978) using A/Duck/Memphis/546/74 H3N2 in both fecal material and nonchlorinated river water. Subsequent to this work, AIV persistence was evaluated in feces (Beard et al., 1984; Lu et al., 2003) and allantoic fluid (Lu et al., 2003) and in all cases
infectivity was relatively short-lived (days). Other than the original work done by Webster et al. (1978), only three studies (Stallknecht et al., 1990b, c; Brown et al., 2007) evaluated the persistence of AIV in water. These studies demonstrated that AIVs (including wild-type and HPAI H5N1 viruses) can persist for extended periods of time in water. Individual viruses differ in their ability to remain infective, and persistence is dependent on water temperature, pH, and salinity, within ranges that are normally encountered with surface water in the field.

The HPAI H5N1 window

The host range for AIV has greatly increased with reports of HPAI H5N1 in wild birds in Eurasia (Sabirovic et al., 2006). These mortality events are significant because they represent the first significant AIV mortality in free-living wild bird species since HPAI H5N3-related mortality in common terns (Sterna hirundo) in South Africa (Becker, 1966). Isolations of HPAI H5N1 are reported from over 60 species of wild birds (Ellis et al., 2004; Chen et al., 2005; Kwon et al., 2005; Liu et al., 2005; Mase et al., 2005; USGS, 2006) and it appears that these viruses may have been transported through Eurasia during migration in 2005. These results reflect a wide range of susceptibility to the HPAI H5N1 Eurasian viruses, but at present, offer little insight into potential wildlife reservoirs. In evaluating these and other host reports it is important to differentiate between a susceptible and reservoir host. There are numerous reported AIV isolations (including HPAI viruses) from birds associated with AIV-infected poultry flocks (Cross, 1987), from captive birds in zoological collections (Ellis et al., 2004), and from wild birds imported for the pet trade (Alexander, 2000). These reported isolations provide evidence of AIV susceptibility and insight regarding anthropogenic activities potentially affecting transmission to wildlife; they do not provide evidence of a wildlife reservoir. Reports of HPAI H5N1 infections in wild birds also may indirectly provide insight into the natural history of wild-type AIVs. Mortality associated with these infections provides a means to detect infection not previously available when studying low pathogenic wild-type viruses. Two relevant observations that emerged as a result of H5N1 surveillance in wild birds are that: 1) the potential host range may be far broader than is evident in the current literature and involve some transmission routes (such as predation) not previously considered; and 2) transmission appears to occur even if the virus is difficult to detect in wild bird populations. The latter observation is extremely important in relation to designing and interpreting results from surveillance efforts directed at these populations.

CONCLUSIONS

Research to date clearly demonstrates that species and population structure are important in AIV maintenance, transmission, and possibly long-distance movement. Differences related to general behavior, spatial and temporal distribution, habitat utilization, migration behavior, population age structure, and individual species susceptibility all potentially influence a species’ role in AIV epidemiology. All of these factors must be understood, or at least considered, when designing surveillance strategies or interpreting surveillance results. The unprecedented mortality associated with HPAI H5N1 infection in wild birds provides a new window from which to view the potential for exchange of AIVs between wild and domestic birds and further demonstrates and expands the varied roles that wild birds may play in AIV epidemiology. These roles must be clearly defined if we are going understand the full implications of current HPAI H5N1 virus introduction into the wild bird populations and most importantly prevent the next one.
LITERATURE CITED


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Received for publication 30 December 2006.