Rice Production Systems and Avian Influenza: Interactions between Mixed-Farming Systems, Poultry and Wild Birds

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Abstract.—Wild waterfowl are the reservoir for avian influenza viruses (AIVs), a family of RNA viruses that may cause mild sickness in waterbirds. Emergence of H5N1, a highly pathogenic avian influenza (HPAI) strain, causing severe disease and mortality in wild birds, poultry and humans, had raised concerns about the role of wild birds in possible transmission of the disease. In this review, the link between rice production systems, poultry production systems, and wild bird ecology is examined to assess the extent to which these interactions could contribute towards the persistence and evolution of HPAI H5N1. The rice (*Oryza sativa*) and poultry production systems in Asia described, and then migration and movements of wild birds discussed. Mixed farming systems in Asia and wild bird movement and migration patterns create opportunities for the persistence of low pathogenic AIVs in these systems. Nonetheless, there is no evidence of long-term persistence of HPAI viruses (including the H5N1 subtype) in the wild. There are still significant gaps in the understanding of how AIVs circulate in rice systems. A better understanding of persistence of AIVs in rice farms, particularly of poultry origins, is essential in limiting exchange of AIVs between mixed-farming systems, poultry and wild birds. *Received 17 March 2008, accepted 15 June 2009.*

Key words.—avian influenza, bird flu, disease, HPAI H5N1, rice agriculture, Southeast Asia, wild birds.

Avian influenza is an important disease of zoonotic origin that has caused morbidity and mortality in domestic animals, wildlife and humans (Muzaffar *et al.* 2006; Olsen *et al.* 2006; Gauthier-Clerc *et al.* 2007). Influenza viruses are divided into three 'types' (A, B or C) based on internal proteins. Influenza viruses that are of epidemiological significance to birds are of type A and are commonly referred to as avian influenza viruses (hereafter AIVs). Surface proteins (hemagglutinin and neuraminidase) that help the virus to enter the host cell are used to further subdivide AIVs into 'subtypes'. At least 16 hemagglutinin and nine neuraminidase variants have been documented, and combinations of hemagglutinin and neuraminidase result in 144 possible subtypes (designated by HxNy notation, where x refers to the xth hemagglutinin variant and y refers to the yth neuraminidase variant). All known AIV subtypes have been recorded from wild waterbirds, which are regarded as the primary reservoirs of AIVs. Each subtype is highly variable in genetic makeup and a given AIV subtype (e.g. H5N1) is best regarded as a complex of viruses (Swayne 2008).

In wild birds, members of the Anatidae (ducks and geese) and Charadriiformes (shorebirds and gulls) are the most common reservoirs of AIV subtypes (Webster *et al.* 1992; Swayne 2000, 2008). Circulation of AIVs in nature involves development of viral infections in juvenile and adult waterbirds and maintenance along migration flyways. Whether AIVs overwinter in the environment is not known, although several studies show that they can be detected in water, sed-

iments and ice (Sivanandan *et al.* 1991; Ito *et al.* 1995; Zhang *et al.* 2006; Lang *et al.* 2008). Differences in methods and contamination of AIV samples, prior to or during laboratory procedures, can pose a serious challenge in the detection of AIVs from the environment, and several studies reporting AIVs in the environment have recently been questioned (Worobey 2008).

Avian influenza viruses are divided into two categories based on their propensity to cause disease in domestic chickens (Alexander 2000). Highly Pathogenic Avian Influenza (HPAI) is caused by AIVs that are extremely virulent, causing up to 100% mortality in domestic chickens. These HPAI viruses are rarely isolated from healthy wild waterfowl and only H5 and H7 subtypes have been found to be highly pathogenic (Swayne 2008). In contrast, most AIV subtypes are benign, causing only minor respiratory disease in their wild hosts or domestic chickens, and are collectively referred to as Low Pathogenic Avian Influenza (LPAI) viruses. Mechanisms that support the evolution of AIVs towards high or low pathogenicity are not known. Ewald and De Leo (2002) predicted that immunologically naïve (and therefore susceptible) hosts, such as genetically-related broiler chickens in poultry farms, would permit the virus to evolve towards HPAI subtypes. In contrast, in wild birds that have been exposed to a diversity of AIV subtypes, selection would favor LPAI subtypes. Although this is indeed seen in wild systems, the mechanisms are not known, and there is no empirical evidence to suggest that evolution cannot occur in the reverse direction (i.e. towards high pathogenicity). Phylogenetic studies on viral subtypes from both wild bird and poultry sources suggest that AIVs evolve as quickly as other similar RNA viruses, although evolution may be faster in poultry (Chen and Holmes 2006).

Outbreaks of the HPAI H5N1 subtype in Southeast Asia since 1997 have differed from previous outbreaks in their ability to cause morbidity and mortality in poultry, wild birds, captive wild animals and humans (Webster *et al.* 2006). The emergence of this virus initially caused global concern over the potential of a human pandemic. Poultry and poultry operations are demonstrably the primary vehicles of virus movement across Eurasia (Webby and Webster 2001; Webster *et al.* 2006; Gauthier-Clerc *et al.* 2007). Although wild birds do not appear to play a major role in the spread of the virus globally, the possibility remains that they may play some role in regions with few poultry (Takekawa *et al.* 2010). Wild birds, poultry and human interactions are key to our understanding of the emergence and dissemination of this virus.

In South and Southeast Asia, poultry production systems are often integrated with other forms of farming. With the loss of natural wetlands, many wild waterfowl species resort to feeding in and around farmland, thereby increasing the chances of intermixing between domestic and wild birds (Boere *et al.* 2006). Avian influenza viruses can exchange genes (reassortment) when host species are co-infected with more than one subtype of the virus, contributing to the evolution of these viruses (Webster *et al.* 2006). Intermixing of domestic and wild birds enhances these opportunities. Bringing together domestic and wild birds in mixed-bird markets also provides favorable conditions for genetic mixing of AIVs (Chen *et al.* 2004; Webster *et al.* 2006).

Few studies have evaluated the role of farming systems on the ecology and evolution of AIVs. In this review, we examine the links between rice (*Oryza sativa*) production, poultry production and wild bird ecology to assess the extent to which these interactions contribute to the persistence and evolution of highly pathogenic AIVs. We first briefly describe the rice and poultry production systems in Asia. We then briefly review the evolution of the HPAI H5N1 subtype. Finally, we examine bird migration and its interactions with rice, poultry and mixed-farming systems to highlight gaps in our understanding of such integrated systems that may result in the persistence of HPAI H5N1.

RICE PRODUCTION SYSTEMS

Asian agriculture is dominated by rice and wheat production (Huke and Huke 1997; Cass-

man 1999; Devendra and Thomas 2002a). In the mid-1990s, paddy rice agriculture occupied about 22% of the world's grain-producing cropland and produced about 29% of the world's grain harvest (FAOSTAT 2006). More than 90% of the world's rice supply is produced in Asia on approximately 86% of the area used for rice production globally (IRRI 1984; FAOSTAT 2006). Over 90% of water channeled through irrigation schemes in Asia is used in rice production (Bhuiyan 1992). Traditional rice production systems in Asia vary among agroecological zones, and can be divided into 1) rain-fed wetlands, 2) irrigated wetlands, 3) rain-fed drylands, 4) irrigated drylands, 5) deepwater rice, 6) tidal swamps, 7) agroforestry areas, and 8) hill agriculture (IRRI 1984). Each production system comprises a complex of land use patterns, cropping patterns, labor and power use, with different environmental and institutional factors affecting crop production. Double- and triple-cropping systems may involve just rice, or rice alternating with other crops. Farming systems are classified differently in different regions or countries, making standardization difficult (Devendra and Thomas 2002a). A variety of remote sensing data, however, has improved our understanding of land use and agricultural patterns at a range of spatial and temporal scales (Fig. 1; Xiao *et al.* 2002, 2006).

The multipurpose use of livestock is integral to crop-animal systems in Asian agriculture (IRRI 1984), and is underestimated in official statistics (Devendra and Thomas 2002b). Agricultural refuse and by-products are used extensively by ruminants and poultry and include cereal straws, sugarcane tops, root crop tops, vines and rice bran. Rice straw is fed to over 90% of domestic ruminants in Asia. Agricultural refuse also provides food for poultry (aquatic and terrestrial) resulting in their integration into mixed-farming systems, adding further to the complexity of Asian agricultural systems.

POULTRY PRODUCTION SYSTEMS

Poultry production is an important part of the global economy (FAO 2001). In many South and Southeast Asian countries, poultry production contributes significantly towards the gross domestic product (Devendra and Thomas 2002a) and is a major protein source for rural households. Poultry production in Southeast Asia was estimated to be 4.2 billion heads in 1996 and was predicted to rise to about 7.4 billion by 2010. Poultry production varies considerably among and within different Asian countries (Fig. 1c), but can be broadly classified into commercial production systems and traditional backyard production systems (FAO 2001).

Commercial systems are further subdivided, based on level of biosecurity and size of operation (FAO 2001; Tiensin *et al.* 2005; Burgos *et al.* 2007), into three sectors: 1) industrial integrated systems, 2) commercial production systems, and 3) small-scale commercial production systems (FAO 2001). Very high levels of biosecurity are maintained in sector 1 systems with strict sanitary and quarantine standards to prevent emergence and transmission of diseases. Sector 1 production systems generally keep breeding stock consisting of up to three generations of birds to maintain healthy birds and reduce introduction of birds from outside sources. When new stock is added to reduce inbreeding, careful quarantine measures prevent introduction of diseases. The size of such operations varies considerably, ranging from 2,000 to 500,000 birds. Sector 2 systems operate under medium to high biosecurity levels, although they may have similar numbers of birds. Diseases are occasionally introduced into these systems with the introduction of new breeding stock. Additionally, the standards for monitoring pathogens (such as LPAI surveillance) are lower compared to Sector 1 systems. Sector 3 is characterized by smaller operations with minimal to low biosecurity levels. Circulating pathogens are usually not monitored and recently-domesticated wild birds are periodically introduced to improve the quality of the breeding stock (Minh and Trong 2007). Various pathogens typically circulate within these systems, frequently giving rise to novel strains that have historically caused disease and mortality in poultry (Swayne 2008). Bird numbers typically range from 50 to 10,000 in these opera-
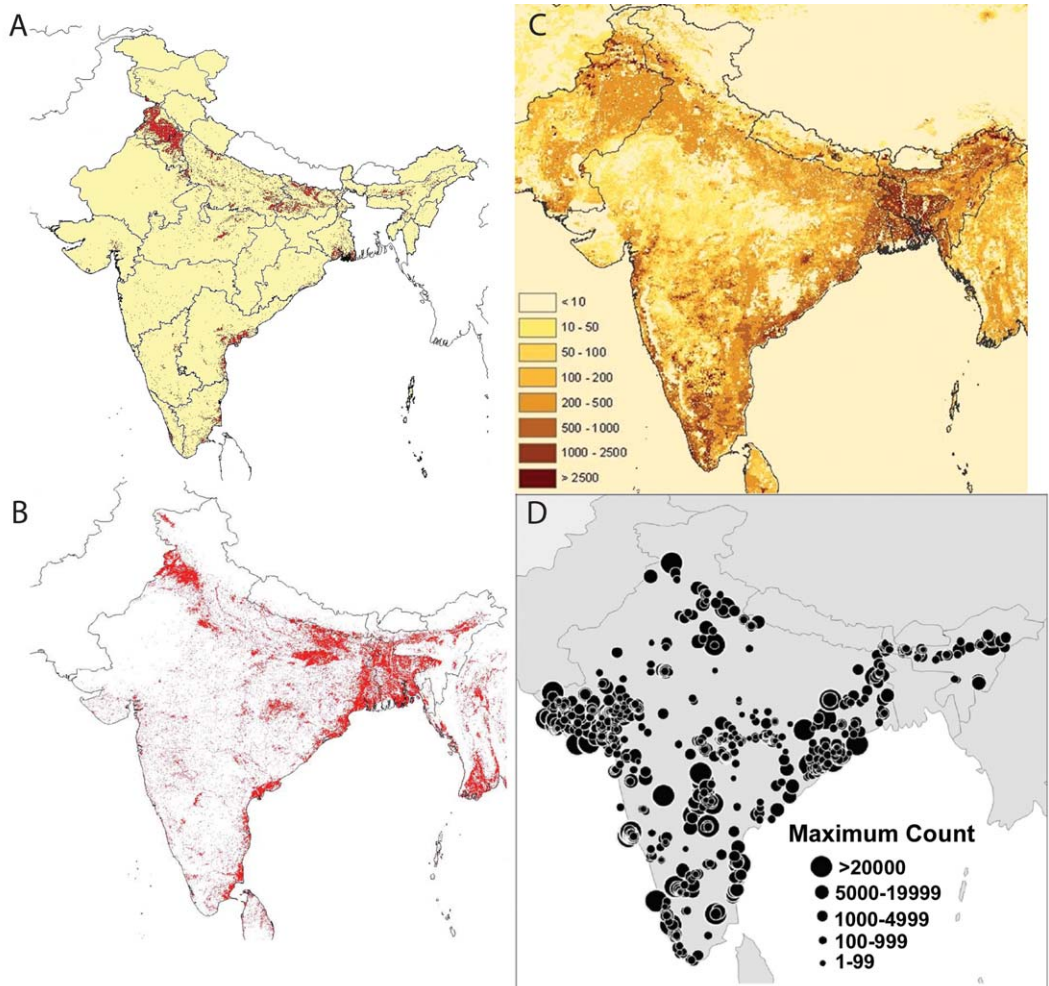
Figure 1. Overlap in the spatial distribution of rice, poultry and wild birds. Shown is the spatial distribution of a) double rice paddies in India (shown in red; X. Xiao, unpublished data), b) all rice paddies in India (in red; from Xiao _et al._ 2006, reproduced with permission from Elsevier), c) poultry density in India (number per km² from FAO 2007), and d) winter distribution and density of migratory waterbirds in India between January and February, 2003-2004 (Li and Mundkur 2007, reproduced with permission from Wetlands International).

tions. As with rice systems, the exact nomenclature and definitions used to classify poultry farming operations vary among nations (FAO 2001; Tiensin _et al._ 2005; Burgos _et al._ 2007).

Backyard poultry production is categorized as the fourth sector in poultry production (FAO 2001). This system is perhaps the most common in much of South and Southeast Asia, with an estimated 60-80% of rural households keeping some form of poultry. This form of production is also widespread elsewhere in Asia, and in Africa and South

America. Backyard poultry consists of various species (e.g. ducks, geese, chickens, guineafowl) that are fed on grain but also actively forage in and around houses, within rice fields (Fig. 2), and in ponds and other water bodies. Birds are of domestic or wild origin, have high levels of genetic diversity (e.g. Minh and Trong 2007), and are kept in enclosures without any biosecurity measures. Other livestock such as goats and cows, as well as pets such as cats and dogs, may intermingle with backyard poultry. Certain backyard poultry (e.g. ducks) are often produced

Figure 2. Herding domestic ducks in a post-harvest rice field, China (JYT photo).

as part of a mixed-farming system, whereby different cohorts are produced in tandem with the cropping cycle so that growing juveniles can feed on crop refuse (e.g. spilled rice) in between crop production cycles thereby reducing feed costs (Devendra and Thomas 2002a; Feare 2006; Gilbert *et al.* 2007; Minh and Trong 2007). Integration of fish, rice and poultry production is a further example of such mixed systems (Minh and Trong 2007; Wood *et al.* 2010). Manure from ducks usually goes directly into fish ponds, enriching the water for plankton growth and thereby aiding fish production (Feare 2006; Minh and Trong 2007). The ducks in these systems may also help to manage pests by feeding on weed seeds and insects in rice fields after the harvest.

EMERGENCE OF HPAI H5N1

The LPAI H5N1 subtype was first detected in domestic geese in Guangdong, China in 1996 and was seemingly widespread in poultry (Webby and Webster 2001; Webster *et al.* 2006). This virus acquired gene segments for internal proteins through reassortments with viruses in Japanese Quail (*Coturnix japonica*; subtype H9N2). The virus also acquired gene segments for hemagglutinin from a goose-like virus (H5N1) and for neuraminidase from ducks (H6N1) leading to the emergence of HPAI H5N1 in 1997 in Hong Kong's poultry markets. The virus became widespread in live poultry markets in

the region and caused 18 human infections, of which six were fatal (Sims *et al.* 2003). The precursors of this virus circulated in Chinese poultry markets and were likely introduced into Hong Kong through live poultry markets (Webby and Webster 2001). This genotype of HPAI H5N1 was eradicated by extensive poultry culls in Hong Kong and has not been detected since (Webster *et al.* 2006).

Since the precursors of the HPAI H5N1 genotype that emerged in Hong Kong continued to circulate in poultry operations in the region, other reassortants (new viruses that have emerged through reassortments) of HPAI H5N1 emerged from goose and duck reservoirs (Guan *et al.* 2002; Chen *et al.* 2004). One genotype of HPAI H5N1 named genotype '*Z*' became dominant and spread across Southeast Asia, with distinct variants dominating in certain countries (e.g. Vietnam and Thailand, Li *et al.* 2004). Subsequently, the deaths of over 6,000 wild birds (including 3,282 Bar-headed Geese *Anser indicus*, 145 Ruddy Shelducks *Tadorna ferruginea*, 1,302 Great Cormorants *Phalacrocorax carbo*, 929 Pallas's Gulls *Ichthyaetus ichthyaetus* and 570 Brown-headed Gulls *Chroicocephalus brunnicephalus*) demonstrated that these genotypes of HPAI H5N1 could cause mortality in wild birds as well as in domesticated stock (Chen *et al.* 2005; Olsen *et al.* 2006).

Records of HPAI H5N1 in wild birds in different geographic localities have helped to intensify the debate about the role of wild birds as reservoirs and vectors of this virus. Although birds may be involved in the spread of the virus in some regions with few poultry, this does not override the much larger risk of the emergence and dissemination of HPAI subtypes due to poultry operations (Olsen *et al.* 2006; Gauthier-Clerc *et al.* 2007; Takekawa *et al.* 2010). Asian mixed-farming systems may indirectly enhance the dissemination of HPAI of poultry origin through increased overlap between wild birds and domestic poultry (Fig. 1; Xiao *et al.* 2006). Migratory birds, particularly ducks, geese and shorebirds, are central to elucidating the role of mixed-farming systems and movement of viruses of poultry and wild bird origin.

WILD BIRD MOVEMENTS

Wild birds of many different species undergo regular migrations driven by breeding instincts, seasonal food availability, altered habitat requirements and weather patterns (Berthold *et al.* 2003). Migratory movements generally have a north-south orientation, with northern hemisphere species wintering in the south and breeding in north temperate areas during summer. Waterfowl and shorebirds characteristically congregate at staging areas prior to, or during, migration in order to build up fat reserves for long flights. En route to their final destinations, they may also stopover in areas for short-term refueling (Warnock *et al.* 2004). Many species do not migrate and remain within defined geographic areas as residents, undergoing local movements in response to food availability and variations in local weather conditions. Immature birds of both migratory and non-migratory species also tend to disperse from their natal areas to seek out future breeding sites. The extent to which immature birds disperse varies considerably both among and within species depending on habitat suitability, resource competition and weather patterns (Baldassarre and Bolen 1994).

Based on predictable migration routes, several overlapping flyways have been recognized throughout the world (Boere *et al.* 2006). These flyways help to simplify the more complex migration patterns observed both within and among species (Ely and Takekawa 1996; Berthold *et al.* 2003; Miller *et al.* 2005; Dobrynina and Kharitonov 2006). Weather may prompt birds to select long flights with few stopovers or short flights with several stopovers (Berthold *et al.* 2003). Migrating birds may also modify their routes based on weather conditions, thereby influencing their arrival times and their final destinations (Miller *et al.* 2005). Changes in land use patterns, local climate and human activity may also affect the short- and long-term migratory patterns of birds (Henny 1973; Ackerman *et al.* 2006; Dobrynina and Kharitonov 2006). In general, migration is an energetically expensive undertaking, potentially leaving individuals immunologically weak and susceptible to morbidity and mortality (Berthold *et al.* 2003).

In Eurasia, flyways that are of particular interest for understanding the long-distance movement of HPAI subtypes include the Baltic Sea-Mediterranean, East African-West Asian, Central Asian and East Asian flyways (Olsen *et al.* 2006). Each of these flyways encompasses a diagonal north-south area, with significant overlap, indicating the potential for birds in different flyways to interact and for movement between flyways. Although generalized flyway maps can aid management decisions (Boere *et al.* 2006), birds using flyways show a range of spatial and temporal patterns that should be addressed in our understanding of disease movements across large geographic areas (Dobrynina and Kharitonov 2006; Gauthier-Clerc *et al.* 2007; Jourdain *et al.* 2007).

WILD BIRDS AND HPAI

The hypothesis that migratory birds are involved in the long-distance movement of HPAI H5N1 was first suggested in 2004 (Gauthier-Clerc *et al.* 2007). The hypothesis that migratory birds are not involved in the long-distance movement of HPAI H5N1 was first challenged in 2004 (Gauthier-Clerc *et al.* 2007) and by the evidence of more than 60 wild bird species found with infections, most of which may be explained as spillover from poultry (reviewed by Olsen *et al.* 2006). There is a wealth of evidence highlighting the role of poultry in the emergence and evolution of HPAI H5N1 from LPAI precursors found in poultry (Chen *et al.* 2004; Duan *et al.* 2007). Dissemination of this virus by migratory waterfowl would require re-introduction of the virus into the wild bird population, in combination with a number of other factors. These include: 1) sustained infections within wild waterfowl without causing illness, 2) the ability of wild birds to fly long distances without eliminating the virus from their bodies, 3) the ability of wild birds to shed viruses enabling transmission during stopovers or at their final destinations, and 4) environmental conditions that enable vi-

ruses to remain viable in the environment (Webster *et al.* 1992; Muzaffar *et al.* 2006; Webster *et al.* 2006; Brown *et al.* 2007).

Generally, re-introduction of HPAI viruses from domestic sources back to the wild is very rare and there is no evidence of long-term persistence of HPAI viruses (including the H5N1 subtype) in the wild (Nettles *et al.* 1985; Webster *et al.* 1992; Swayne 2008). Wild waterfowl can carry LPAI viruses over long distances, but most records of HPAI H5N1 infections from wild birds to date were from severely morbid or dead individuals, suggesting the same does not occur in HPAI viruses (Olsen *et al.* 2006). Viral shedding in the feces of infected birds exposes wild birds in the same habitat (particularly waterbirds in aquatic habitats) to viruses. Avian influenza viruses of various LPAI subtypes can remain infective for 30-207 days depending on water temperatures and salinities (Webster *et al.* 1978; Stallknecht *et al.* 1990; Brown *et al.* 2007). Generally, lower water temperatures (4-17°C) increase persistence of LPAI subtypes in water (Stallknecht *et al.* 1990; Brown *et al.* 2007). Experimental studies reveal that HPAI H5N1 survive for 17-30 days depending on conditions, which is much shorter than for LPAI H5 subtypes, suggesting that prolonged persistence to permit cycling between wild birds is less likely (Brown *et al.* 2007). We are aware of one study that detected and partly identified viral HA subtypes from water and sediments (Lang *et al.* 2008), but there is no information on the viability of AIVs collected. To what extent wild waterfowl contribute to the dissemination of HPAI H5N1 therefore remains unknown. The occurrence of infections of wild birds usually has been in conjunction with outbreaks in poultry, and transmission of HPAI H5N1 from poultry to wild birds is not disputed (Gauthier-Clerc *et al.* 2007). A few cases of infections in wild birds in the absence of poultry operations (such as at Erkhel Lake, Mongolia in 2005) suggests that some transmission may result from wild bird movements (Chen *et al.* 2005, 2006; Gauthier-Clerc *et al.* 2007).

Experimental infection with HPAI H5N1 in captive waterfowl show high susceptibility in swans (*Cygnus* spp.) with 100% mortality in all species tested (Brown *et al.* 2008). Other waterbird species also show significant illness and even death when infected experimentally (e.g. Bar-headed Goose, American Herring Gull *Larus smithsonianus*), while others do not exhibit any clinical signs of disease (e.g. Mallard *Anas platyrhynchos*, Northern Pintail *Anas acuta*, Redhead *Aythya americana* and Blue-winged Teal *Anas discors*) (Brown *et al.* 2006, 2008). Domestic waterfowl may develop partial immunity when they have been vaccinated for other circulating viruses, thereby providing protection against HPAI viruses (Webby and Webster 2001). Domestic Mallards, in particular, can remain infectious without showing clinical signs of illness and may be an important vehicle in the spread of HPAI viruses to wild birds (Strum-Ramirez *et al.* 2004), especially where intermingling opportunities are abundant (as in mixed-farming systems). Other species that occur in Asia and have passed clinical infections without apparent illness, such as pintail and teal species, also need to be examined for their potential as vectors of HPAI viruses.

HPAI-infected waterbirds may not be able to migrate over long distances without succumbing to illness (Muzaffar *et al.* 2006; Olsen *et al.* 2006; Gauthier-Clerc *et al.* 2007). Bird migration is energetically expensive accompanied with immune-suppression that often results in mortality of migrants (Greenberg and Marra 2005). However, satellite telemetry studies may help in establishing whether birds can withstand long distance flights after being infected. For instance, Gaidet *et al.* (2008) recorded the migration of healthy White-faced Whistling Ducks (*Dendrocygna viduata*) and Spur-winged Geese (*Plectropterus gambensis*) fitted with satellite transmitters in northern Nigeria. These birds were also swabbed for HPAI subtypes at the time of capture and subsequently two individuals, one of each species, tested positive for HPAI H5N2, another well-known HPAI subtype that has caused poultry deaths in the past (Swayne 2008). The White-faced Whistling Duck migrated from Nigeria northwest to western Chad covering a dis-

tance of over 300 km, illustrating that wild waterfowl may indeed fly long distances without succumbing to infections of HPAI H5N2 (Gaidet *et al.* 2008). Although H5N2 is very different from H5N1, this study underscores the need to examine waterfowl movement patterns in relation to HPAI H5N1. Additionally, satellite telemetry studies on migration patterns of wild waterfowl and movement patterns of free-ranging domestic ducks can provide evidence of interactions that could lead to the exchange of AIVs between wild and domestic ducks (Gaidet *et al.* 2008; authors' unpublished data). These methods in conjunction with viral surveillance could provide clues to the nature and risk of AIV transmission between wild and domestic systems.

RISKS OF AIV TRANSMISSION

Agricultural practices alone may attract greater numbers of birds in manmade ecosystems, such as rice fields (e.g. Elphick and Oring 1998; Ackerman *et al.* 2006; Swayne 2008). Transmission of a range of diseases (e.g. avian cholera in the United States) has been documented in waterbirds, particularly in managed wetland or agricultural ecosystems (Friend and Franson 1999). One potential mechanism for the re-introduction of HPAI viruses into wild birds could be entry via integrated agricultural and poultry production systems due to their overlap with wild bird distributions.

As for other grain crops, modern rice cultivars are products of thousands of years of domestication and are, in essence, wetland plants with adaptations to survive best under periodically flooded conditions (Baki *et al.* 2000). Flooded rice fields are suitable habitat for many arthropods, molluscs and small vertebrates, which in turn attract many species of wild birds, particularly waterfowl, wading birds and shorebirds. After harvest, rice fields continue to be very important feeding areas for wild birds due to the large amounts of post-harvest refuse, including seeds and husks as well as invertebrates and small vertebrates (Miller *et al.* 1989; Devendra and Thomas 2002a). Some wild birds,

such as Greater White-fronted Geese (*Anser albifrons*), may actually select rice fields over natural wetlands for foraging (Ackerman *et al.* 2006). These characteristics of rice fields also make them unusual compared to other crops, especially for their potential in disease transmission. Defecation by foraging wild birds likely enables the persistence of AIVs in these areas. Repeated use of flooded areas by wild birds at relatively cool temperatures is likely to ensure a constant supply of infective viral particles. Since wild LPAI subtypes can persist for variable periods under variable, but generally cool, temperatures (Webster *et al.* 1978; Stallknecht *et al.* 1990; Brown *et al.* 2007), flooded rice fields used by wild waterbirds could form an important reservoir of LPAI viruses. Lowest water temperatures, which are most appropriate for prolonged persistence of many wild AIVs, occur in South and Southeast Asia from November to January (IRRI 1984). The timing coincides with the period (October to March) when thousands of migratory waterbirds pass through or winter in these areas (Li and Mundkur 2007; Fig. 1d), many of them foraging in rice fields. Some wild birds might help in cycling LPAI subtypes in water associated with rice fields, although supporting evidence for this relationship is not currently available.

The potential link between rice fields, poultry and wild birds in AIV transmission is hypothesized from poultry outbreak locations and their proximity to wild birds in various farming systems (Olsen *et al.* 2006; Webster *et al.* 2006; Gauthier-Clerc *et al.* 2007; Gilbert *et al.* 2007; Xiao *et al.* 2007). However, a direct link has not been established since the persistence of AIVs has not been studied in mixed-farming systems. Poultry and wild waterfowl presence in rice fields during the post harvest period may facilitate the exchange and persistence of AIV subtypes. For example, in mixed cropping systems, the first rice crop is sown prior to the arrival of the rainy season, while second and third crops are transplanted into the same fields after the first crop has been harvested (IRRI 1984; Fig. 3). Both chickens and ducks are allowed to forage for agricultural waste grains
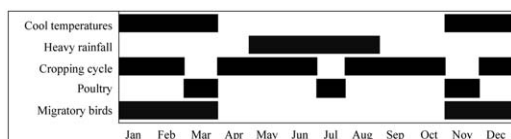
Figure 3. A typical cropping cycle in South Asia in relation to temperature, rainfall and abundance of poultry and migratory birds. Cool temperatures refer to periods with temperatures suitable for persistence of HPAI subtypes in the environment. 'Cropping cycle' shows the planting (shaded) and post-harvest periods (unshaded) of crops. Poultry and migratory birds forage in fields during designated periods (shaded) corresponding with post-harvest and wintering periods, respectively. Periods where cool temperatures overlap with foraging poultry and migratory birds (Mar and Nov in this schematic) are likely to be most important for the exchange and possible persistence of AIVs.

and invertebrates within the paddy fields during the periods between crops (Devendra and Thomas 2002a). Avian influenza viruses can remain viable in chicken manure at warmer temperatures (15-20°C) for up to six days, although viability could vary among subtypes (Lu *et al.* 2003). At cooler temperatures (4°C), AIVs in chicken manure may remain viable for as long as 20 days (Lu *et al.* 2003), providing ample opportunity for infections to circulate among freely grazing poultry. In a triple-cropping system, up to two of these post-harvest periods could overlap with migratory bird activity, lending the opportunity for exchange and persistence of AIVs between poultry and wild waterfowl (Fig. 3).

Interactions between poultry and wild birds also occur during the cropping cycle, especially when domestic ducks forage within planted rice crops and in adjacent wetlands (FAO 2001; Minh and Trong 2007; Xiao *et al.* 2007). Duck production in Vietnam, for instance, involves rice-duck systems integrated with fish production, and ducks forage in fish ponds and nearby wetlands during the rainy season (Minh and Trong 2007). Domestic duck populations in Vietnam are second only to those in China and vast flocks of ducks regularly venture into both rice fields and wetland areas. Since persistence of LPAI subtypes in water tends to last longer compared to that in manure or other dry conditions (Lu *et al.* 2003; Brown *et*

al. 2007), the movement of domestic ducks in and out of wetlands may constitute an important step in reintroducing AIVs from poultry into wild systems.

Whether HPAI subtypes can persist in rice fields and wetlands is not known. Considerable temporal and spatial overlap occurs between wild waterfowl and domestic ducks in Poyang Lake, Jiangxi Province, China (Chen *et al.* 2006; Webster *et al.* 2006) and quantitative information on the extent of such overlap is currently being gathered (authors' unpublished data). Poyang Lake is also one of the sites where wild bird mortality has been documented as a result of HPAI H5N1 infections (Chen *et al.* 2006), suggesting that the virus must have persisted long enough to allow wild birds to become infected. Given the adaptability of the viruses, the absence of biosecurity in mixed-farming systems, the ability of some domestic ducks (e.g. Mallards) to harbor HPAI H5N1 without showing clinical signs, and the frequent movement of ducks between wild and domestic ecosystems, it is no surprise that such a re-introduction of HPAI into wild birds had occurred in Poyang Lake. Whether HPAI H5N1 might further adapt so that it can persist for longer durations in environments such as rice fields and wetlands, thereby allowing persistent endemic cycles with wild waterbirds to develop, remains to be determined.

SUMMARY AND CONCLUSIONS

Avian influenza viruses are common in nature and circulate among waterbirds of various species in the form of LPAI subtypes. The evolution of HPAI subtypes from LPAI subtypes has been documented many times in domestic poultry but their re-introduction into wild birds has been rare. In most cases, there has been no evidence of long-term persistence of the HPAI subtypes (including H5N1) in cycles involving wild birds. Rice production systems are especially important for understanding the links between different forms of avian influenza because of their similarities with semi-aquatic ecosystems where AIVs can persist. Rice production, when inte-

grated with poultry production, forms an especially important avenue through which wild birds and domestic birds may overlap in their temporal and spatial distributions. At such interfaces, transmission of AIVs is likely to occur in both directions, although for the case of HPAI viruses, the direction is more likely to be from domestic to wild birds rather than the reverse. Satellite telemetry studies provide a wealth of information on migration patterns of wild and free-ranging domestic waterfowl. These methods in conjunction with remotely sensed data on poultry and rice production systems may aid in providing an understanding of the dynamics of such interfaces. Environmental sampling to detect viral particles in water and sediments could elucidate persistence patterns of AIVs in wild birds. The ecology and evolution of AIVs in wild and manmade systems is not well understood. As of now, wild birds are threatened by HPAI H5N1, a subtype that has evolved in poultry. Wild birds therefore require protection from exposure to this virus at the domestic-wild bird interfaces in integrated agricultural systems in Asia. The vast network of agricultural production systems, the widespread occurrence of backyard poultry and the socioeconomic conditions of people involved in such systems do not lend an immediate solution to this problem.

Continued studies on the ecological aspects of this virus and its various genotypes are therefore essential in our attempt to manage the disease in wild birds. The research should include studies on: 1) susceptibility of various wild hosts that frequently interact with domestic or wild-caught poultry, 2) environmental testing for AIVs, particularly of water in flooded rice fields and their surroundings in mixed-farming systems, 3) understanding and limiting interactions between wild waterbirds and domestic poultry in mixed-farming systems, 4) mechanisms of evolution of LPAI to HPAI in the wild, 5) evaluation of the role of wild birds in the spread of HPAI viruses through satellite telemetry studies combined with viral sampling, and 6) mechanisms of persistence of AIVs, particularly HPAI subtypes, in wild reservoirs and in the environment.

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