

Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America

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Abstract

Prior to the emergence of the A/goose/Guangdong/1/1996 (Gs/GD) H5N1 influenza A virus, the long-held and well-supported paradigm was that highly pathogenic avian influenza (HPAI) outbreaks were restricted to poultry, the result of cross-species transmission of precursor viruses from wild aquatic birds that subsequently gained pathogenicity in domestic birds. Therefore, management agencies typically adopted a prevention, control, and eradication strategy that included strict biosecurity for domestic bird production, isolation of infected and exposed flocks, and prompt depopulation. In most cases, this strategy has proved sufficient for eradicating HPAI. Since 2002, this paradigm has been challenged with many detections of viral descendants of the Gs/GD lineage among wild birds, most of which have been associated with sporadic mortality events. Since the emergence and evolution of the genetically distinct clade 2.3.4.4 Gs/GD lineage HPAI viruses in approximately 2010, there have been further increases in the occurrence of HPAI in wild birds and geographic spread through migratory bird movement. A prominent example is the introduction of clade 2.3.4.4 Gs/GD HPAI viruses from East Asia

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to North America via migratory birds in autumn 2014 that ultimately led to the largest outbreak of HPAI in the history of the United States. Given the apparent maintenance of Gs/GD lineage HPAI viruses in a global avian reservoir; bidirectional virus exchange between wild and domestic birds facilitating the continued adaptation of Gs/GD HPAI viruses in wild bird hosts; the current frequency of HPAI outbreaks in wild birds globally, and particularly in Eurasia where Gs/GD HPAI viruses may now be enzootic; and ongoing dispersal of AI viruses from East Asia to North America via migratory birds, HPAI now represents an emerging disease threat to North American wildlife. This recent paradigm shift implies that management of HPAI in domestic birds alone may no longer be sufficient to eradicate HPAI viruses from a given country or region. Rather, agencies managing wild birds and their habitats may consider the development or adoption of mitigation strategies to minimize introductions to poultry, to reduce negative impacts on wild bird populations, and to diminish adverse effects to stakeholders using wildlife resources. The main objective of this review is, therefore, to provide information that will assist wildlife managers in developing mitigation strategies or approaches for dealing with outbreaks of Gs/GD HPAI in wild birds in the form of preparedness, surveillance, research, communications, and targeted management actions. Resultant outbreak response plans and actions may represent meaningful steps of wildlife managers toward the use of collaborative and multi-jurisdictional One Health approaches when it comes to the detection, investigation, and mitigation of emerging viruses at the human-domestic animal-wildlife interface.

KEYWORDS

avian influenza, bird flu, disease, highly pathogenic, influenza, outbreak, North America, wildlife

All influenza A viruses, including those that cause bird flu, swine flu, and (human) seasonal influenza, belong to the same viral taxonomic species. The greatest genetic and antigenic diversity of influenza A viruses is maintained in birds. This review is focused on avian-origin influenza A (AI) viruses in birds, specifically those considered to be highly pathogenic (HP) in poultry. Prior to 2002, highly pathogenic avian-origin influenza (HPAI) viruses were limited almost exclusively to poultry and disease resulting from such an infection had only been documented once in wild birds (Rowan 1962, Becker 1966). The situation has since changed. Following the emergence of a specific viral lineage in domestic geese in Guangdong, China in 1996, there have been increasing detections of HPAI viruses, often associated with mortality in wild birds. In this review our objective is to provide basic background information on AI viruses with an emphasis on those affecting wild birds, a brief history of the emergence and evolution of

goose/Guangdong (Gs/GD) lineage HPAI viruses that have recently affected wild birds including those inhabiting North America, a perspective on the ongoing maintenance of Gs/GD lineage HPAI viruses in a global avian reservoir as it pertains to the potential for future outbreaks of HPAI in North American wildlife, and information that wildlife agencies or managers can use to prepare for and respond to future outbreaks of HPAI in wild birds.

BACKGROUND ON AVIAN-ORIGIN INFLUENZA A VIRUSES

Wild aquatic birds including waterfowl, shorebirds, gulls, and seabirds are the primary or primordial reservoir hosts of the greatest genetic and antigenic diversity of influenza A viruses (Olsen et al. 2006, Lang et al. 2016). Influenza A viruses maintained in wild birds are not typically associated with disease in these hosts; however, disease sometimes occurs when wild bird-origin viruses spread to other vertebrate species. For example, outbreaks of influenza in wild harbor seals (*Phoca vitulina*) and farmed mink have been attributed to viruses of wild-bird origin (Hinshaw et al. 1984, Klingeborn et al. 1985, Berg et al. 1990, Anthony et al. 2012, Zohari et al. 2014). Evidence for human exposure to AI viruses maintained in wild birds is sparse (Gill et al. 2006). Conversely, there is substantial evidence that AI viruses maintained in wild birds are sporadically introduced to domestic poultry (Figure 1) where they sometimes adapt to and are maintained among domestic birds (Swayne 2008). On rare occasions, viruses are again transmitted between species, this time from domestic poultry to humans (Figure 1) where they may cause clinical disease (Lam et al. 2013). Other times, as part of the host adaptation process, AI viruses that have a hemagglutinin gene of the H5 or H7 subtype may develop a HP phenotype in domestic birds. That is, viruses develop the propensity to cause mortality in chickens as assessed through a standardized pathogenicity index involving experimentally inoculated 6-week-old specific-pathogen-free chickens (Allan et al. 1977, Swayne and Suarez 2000).

Historically (i.e., prior to 2002), HPAI infections were only associated with domestic birds with the exception of a single outbreak among terns (*Sterna* spp.) in South Africa in 1961 (Becker 1966, Rowan 1962; Figure 2). The complete epidemiological context of this wild bird mortality event is not clear from published accounts, but the HPAI viruses leading to disease in terns may have developed pathogenicity in domestic poultry (e.g., chickens, ostriches) raised within this region. Since 2002, the detection of HPAI viruses in wild birds has become more

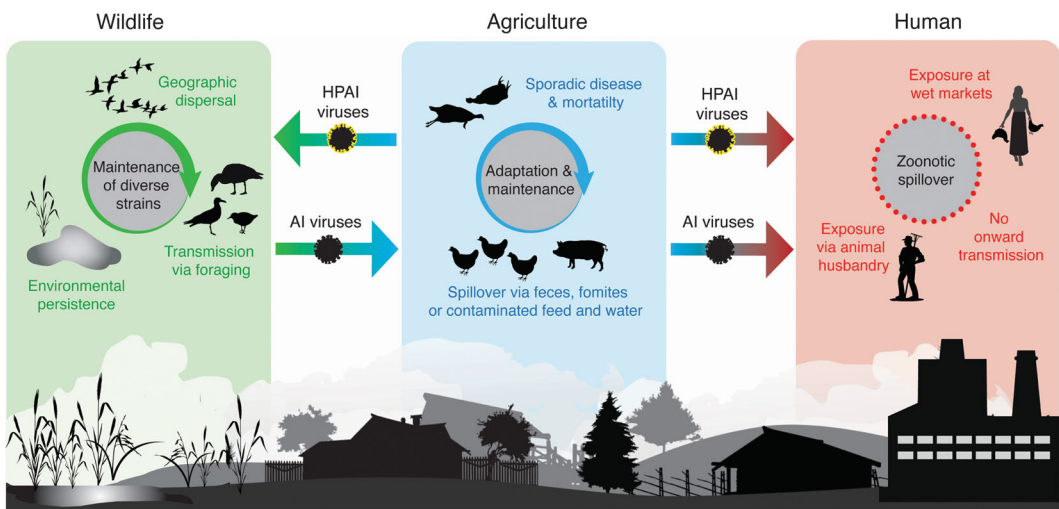


FIGURE 1 Conceptual diagram depicting the generalized ecology of avian-origin influenza A (AI) viruses. Arrows depict common directionality of cross-species transmission events for AI viruses, including those with a highly pathogenic (HP) phenotype among wildlife, agricultural, and human sectors

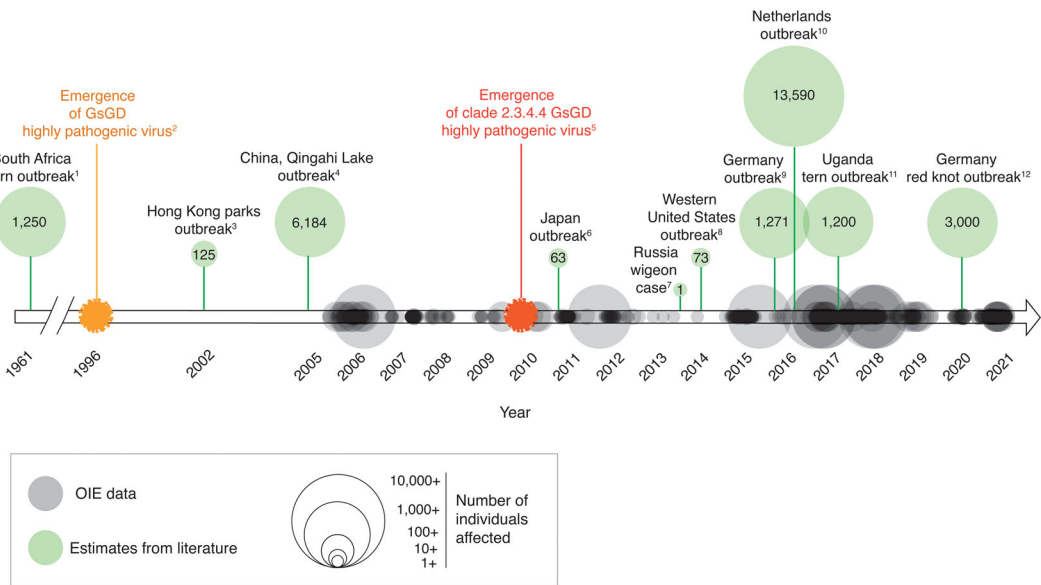


FIGURE 2 Timeline depicting occurrence and magnitude of outbreaks of highly pathogenic avian influenza (HPAI) in wild and captive birds (i.e., non-poultry), as reported to the World Organisation for Animal Health (OIE) and in representative published reports, relative to the evolution of goose/Guangdong (GsGD) lineage HPAI viruses. Apparent differences in reported outbreak magnitudes between OIE data and published accounts reflect different methods for outbreak characterization and reporting among organizations and administrative regions. Data courtesy of the World Organisation for Animal Health (OIE 2021a) and references reported in literature cited (¹Rowan 1962, ²Guo et al. 1998, ³Ellis et al. 2004, ⁴Chen et al. 2006, ⁵Smith et al. 2015, ⁶Sakoda et al. 2012, ⁷Marchenko et al. 2015, ⁸Bevins et al. 2016, ⁹Pohlmann et al. 2018, ¹⁰Kleyheeg et al. 2017, ¹¹Abolnik et al. 2019, ¹²European Food Safety Authority et al. 2021)

common (Figures 2–3). The majority of cross-species transmission of HPAI viruses between poultry and wild birds has involved a particular viral genetic lineage that first emerged in domestic geese in Guangdong, China.

EMERGENCE AND EVOLUTION OF GOOSE/GUANGDONG LINEAGE HPAI VIRUSES

In the spring of 1996, domestic geese in Guangdong, China were affected by HPAI associated with hemorrhagic, neurological disease and mortality exceeding 40%. The causal agent was identified as an HPAI virus strain designated as A/goose/Guangdong/1/1996 (H5N1) (Wan 2012). In 1997, viral descendants of A/goose/Guangdong/1/1996 (H5N1) were identified among domestic chickens during HPAI outbreaks in Hong Kong and from 18 human patients, 6 of whom died (Guo et al. 1998, Xu et al. 1999, Sims et al. 2003). Despite the depopulation of domestic birds on affected farms and the introduction of new controls in local poultry markets, A/goose/Guangdong/1/1996-like (Gs/GD) viruses were maintained among domestic birds within the region, leading to additional sporadic poultry outbreaks (Cauthen et al. 2000).

In late 2002 and early 2003, Gs/GD HPAI viruses were associated with the mortality of wild and captive aquatic birds (e.g., waterfowl, herons, gulls, and flamingos) in Hong Kong parklands representing the first reported detections of HPAI in wild birds since 1961 (Ellis et al. 2004; Figure 2). Though unknown at the time, these detections in 2002–2003 marked the first of many new challenges to the long-held and well-supported paradigm that HPAI was a poultry disease that could be effectively eradicated through the implementation of strict biosecurity for domestic bird production and prompt detection and depopulation of infected and exposed flocks.

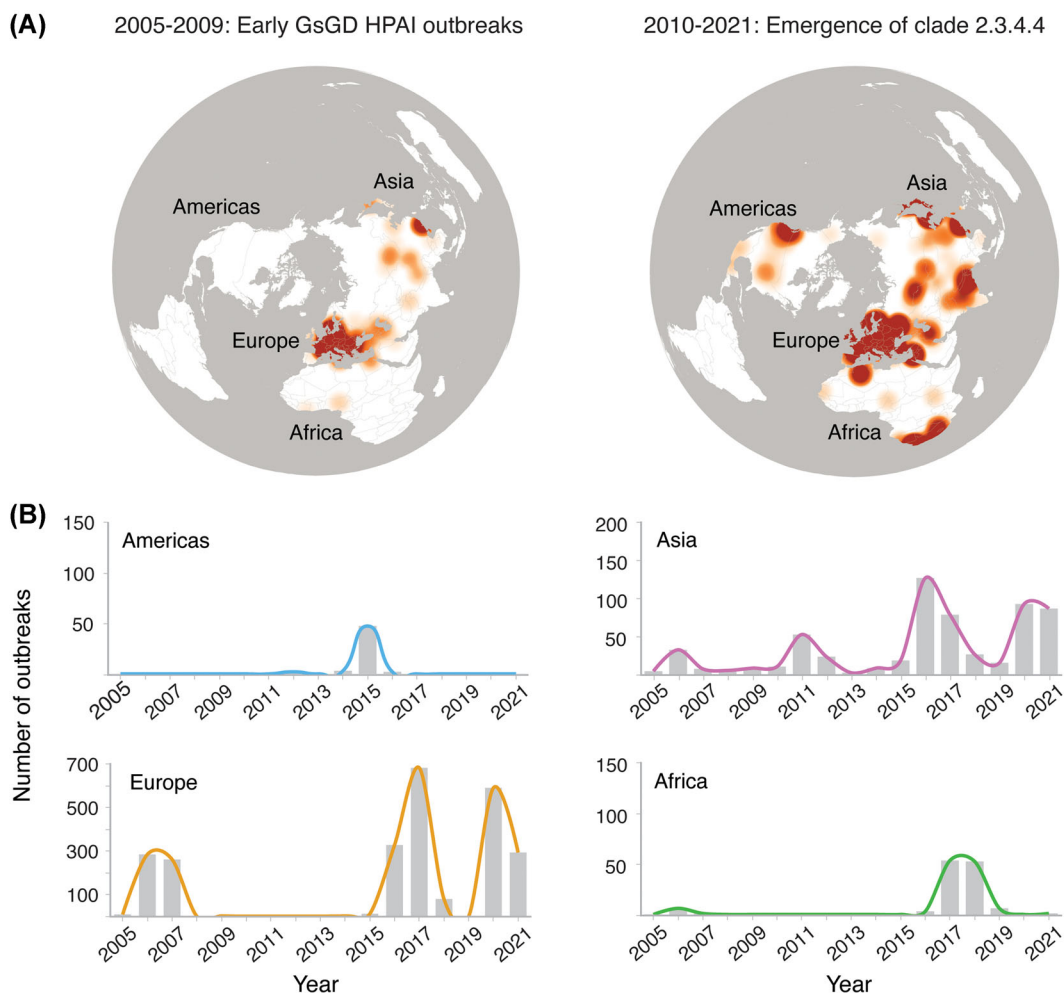


FIGURE 3 Occurrence of outbreak events for highly pathogenic avian influenza (HPAI) in wild and captive birds (i.e., non-poultry) from 2 August 2005–22 March 2021 as reported to the World Organisation for Animal Health (OIE). Panel A depicts the relative occurrence of detection events (red) geographically during the period following spread of emergent A/goose/Guangdong/1/1996-like (GsGD) highly pathogenic HPAI viruses to wild and captive birds (left) and subsequent to the evolution of clade 2.3.4.4 viruses (right), many of which may be adapted to wild birds. Panel B depicts the relative occurrence of HPAI outbreak detections by year. Data courtesy of the World Organisation for Animal Health (OIE [2021a](https://www.oie.int/))

By early 2004, periodic outbreaks of Gs/GD HPAI expanded beyond Hong Kong to 8 Asian countries (Sims et al. 2005). Also during this time interval, Gs/GD HPAI viruses were again reported to cause fatal human disease, emphasizing the zoonotic risk of these avian-origin viruses (Peiris et al. 2004).

In 2005, Gs/GD HPAI viruses were associated with an outbreak at Qinghai Lake, China that resulted in the mortality of more than 6,000 wild aquatic birds, including large numbers of bar-headed geese (*Anser indicus*), brown-headed gulls (*Chroicocephalus brunnicephalus*), and great black-headed gulls (*Larus ichthyaeetus*; Chen et al. 2006; Liu et al. 2005; Figure 2). By late 2005, Gs/GD HPAI viruses had spread to wild birds in eastern Europe, purportedly through the transport of infected poultry and dispersal via wildlife (Gilbert et al. 2006; Ward et al. 2008, 2009). During 2006–2009, Gs/GD HPAI viruses proliferated throughout at least 38 countries in Africa, Asia, Europe, and the Middle East (Figure 3) with many detections in wild and domestic birds. Affected wild bird taxa included ducks,



swans, geese, gulls, crows, and raptors (Brown 2010). It is plausible that 1 genetic lineage of viral diversity (clade 2.3.2.1) was, at least partially, maintained within, dispersed by, and adapted to wild birds during this interval. The global trade of infected domestic poultry and spread of viruses to wild birds were purported to be the most important mechanisms governing the occurrence of Gs/GD HPAI viruses within the global avian reservoir (i.e., birds in which viruses were maintained) during this period (WHO/OIE/FAO H5N1 Evolution Working Group 2012). Furthermore, human cases of disease due to infection with Gs/GD HPAI viruses continued during this time period (many of which were fatal), though exposure was generally associated with poultry contact (Wan et al. 2011). One exception was a cluster of 7 human cases in Azerbaijan during 2006 (4 of which were fatal) for which de-feathering of infected dead wild swans (*Cygnus* spp.) was considered the most likely source of infection (Gilsdorf et al. 2006).

From 2010–2013, sporadic outbreaks caused by Gs/GD HPAI viruses continued to affect wild and domestic birds in Asia and Europe (Marchenko et al. 2011, Marinova-Petkova et al. 2012, Sakoda et al. 2012, Luo et al. 2018). A specific viral lineage of Gs/GD HPAI viruses emerged during this time period, clade 2.3.4.4 viruses (Smith et al. 2015). These clade 2.3.4.4 Gs/GD HPAI viruses would ultimately become further adapted to waterfowl, sometimes causing apparent asymptomatic infections (Kwon et al. 2017, Pantin-Jackwood et al. 2017, van den Brand et al. 2018, Seekings et al. 2021), and exhibit limited capacity for transmission to mammals (Kaplan et al. 2016, Herfst et al. 2018). In early 2014, clade 2.3.4.4 Gs/GD HPAI viruses were identified as causing widespread outbreaks of disease in both wild waterfowl and domestic poultry in South Korea (Jeong et al. 2014). The detection of a clade 2.3.4.4 Gs/GD HPAI virus in an Eurasian wigeon (*Mareca penelope*) in northeastern Russia, coincident with the onset of autumn migration during September 2014 (Marchenko et al. 2015), foreshadowed an unprecedented event to follow to the east.

Concomitant with the southward migration of migratory waterfowl in late November 2014, HPAI viruses were detected in wild birds inhabiting the United States and Canada for the first time in recorded history (Lee et al. 2015). Clade 2.3.4.4 Gs/GD HPAI viruses were first detected in poultry within a region of southern British Columbia, Canada, that serves as important staging and wintering habitat for large numbers of migratory waterfowl and shorebirds (Pasick et al. 2015). Soon after, HPAI was detected in wild waterfowl and captive falcon carcasses recovered in northern Washington, USA, the latter birds having recently fed upon a captured American wigeon (*Mareca americana*) prior to expiring (Ip et al. 2015). The best available evidence suggests that Gs/GD HPAI viruses were introduced from East Asia to North America via Alaska by wild birds with extensive reassortment, or the genetic shuffling of viral genes, between these HPAI viruses and other AI viruses maintained in North American wild birds following viral introduction (Lee et al. 2016; Hill et al. 2017; Ramey et al. 2016, 2017). Subsequently, an outbreak of Gs/GD HPAI affected wild waterfowl and raptors, and domestic chickens and turkeys in areas throughout the western and central United States and Canada through June 2015 (Bevins et al. 2016, Krauss et al. 2016). This outbreak resulted in the loss of an unknown number of wild birds, >50 million domestic birds (Ramos et al. 2017), and approximately \$3 billion dollars in agricultural-related damages (indemnity payments, costs of response activities, lost revenue) in the United States alone (Greene 2015, Hagerman and Marsh 2016). No cases of human infection with clade 2.3.4.4 Gs/GD HPAI viruses were identified in North America during this outbreak. Though clade 2.3.4.4 Gs/GD HPAI viruses appeared to be eradicated in domestic poultry within the United States and Canada by early October 2015 through aggressive mitigation efforts (e.g., depopulation of poultry), there is evidence that HPAI viruses of this viral lineage continued to be maintained in wild birds and the wetland environments they inhabited within North America through at least November 2016 (Lee et al. 2017b, 2018).

Concurrent with outbreaks of HPAI in North America during 2014–2015, Europe also experienced numerous detections of Gs/GD HPAI viruses in wild, captive, and domestic birds, purportedly, at least in part, a function of wild bird-mediated viral dispersal from Asia (Harder et al. 2015, Verhagen et al. 2015, Globig et al. 2017). By 2016–2017, detections of clade 2.3.4.4 Gs/GD HPAI viruses in wild and domestic birds had become even further widespread in Europe, Africa, and Asia (Abolnik et al. 2019, Poen et al. 2019, Lycett et al. 2020). Though Gs/GD HPAI viruses have not been detected in wild birds inhabiting North America since 2016, there have been ongoing outbreaks of Gs/GD HPAI in wild birds (e.g., crows, ducks, swans, geese, gulls, and raptors) and domestic poultry in Asia and Europe, and sporadic outbreaks in Africa, throughout 2018–2020 (Figure 3) and continuing into 2021 (Poen et al. 2019,



Molini et al. 2020, Baek et al. 2021, European Food Safety Authority et al. 2021, Verhagen et al. 2021). These recent outbreaks have, at times, resulted in disease and mortality of fairly large numbers of birds (e.g., >10,000 individuals) and affected diverse species including African penguin (*Spheniscus demersus*; Molini et al. 2020), bar-headed goose, barnacle goose (*Branta leucopsis*), black-necked grebe (*Podiceps nigricollis*), brown-headed gull, Eurasian wigeon, great black-backed gull (*Larus marinus*), great black-headed gull, mute swan (*Cygnus olor*; Hill et al. 2019), red knot (*Calidris canutus*), tufted duck (*Aythya fuligula*), peregrine falcon (*Falco peregrinus*), white-tailed eagle (*Haliaeetus albicilla*; Krone et al. 2018), and white-winged terns (*Chlidonias leucopterus*; Kleyheeg et al. 2017, Li et al. 2017, Abolnik et al. 2019, European Food Safety Authority et al. 2021, World Organisation for Animal Health [OIE] 2021c). Wild bird-origin clade 2.3.4.4 Gs/GD HPAI viruses have also been implicated in recent reports of cross-species transmission to mammalian wildlife including gray seals (*Halichoerus grypus*), harbor seals (*Phoca vitulina*), and red fox (*Vulpes vulpes*; Shin et al. 2019, OIE 2021b, Rijks et al. 2021). Reports of human infection with clade 2.3.4.4 Gs/GD HPAI viruses have so far been sporadic, with exposures generally associated with domestic poultry contact (e.g., those in China and Russia; Yang et al. 2015, Bi et al. 2016, He et al. 2018, Pyankova et al. 2021).

Recent increases in detections of HPAI in wild birds and other wildlife (since 2002) do not appear to be primarily a function of increased awareness of this disease, enhancements in surveillance effort, or the development of improved molecular diagnostics. For example, following the identification of HPAI in terns in South Africa in 1961, many research and surveillance efforts had been conducted to understand ecology of AI viruses in natural reservoir wild bird species leading up to detections in Hong Kong in 2002 (Stallknecht 2003), yet none reported HPAI in wild birds, even when sampling was conducted in association with poultry outbreaks (Nettles et al. 1985). Following the detections of HPAI in captive and wild birds in Hong Kong and China in 2002–2005, large-scale active surveillance programs were established in Europe and North America. Since the establishment of these programs, most detections of HPAI in wild birds have been spatiotemporally coincident with outbreaks of poultry disease or wild bird mortality events (Hesterberg et al. 2009, Bevins et al. 2016) with few exceptions (Lee et al. 2017b), despite substantial investment in the sampling of many thousands of apparently healthy or hunter-harvested wild birds and the application of contemporary molecular diagnostics (Bevins et al. 2014). Also, well-established surveillance efforts in Australia and South America have not yet reported the detection of Gs/GD HPAI in wild birds, providing evidence that such viruses have not yet been dispersed to these continents via wild bird migration (Pereda et al. 2008, Grillo et al. 2015, Jiménez-Bluhm et al. 2018).

POTENTIAL FOR FUTURE OUTBREAKS OF HPAI IN NORTH AMERICAN WILDLIFE

Though the occurrence, timing, and extent of future outbreaks of HPAI in North American wildlife are uncertain and will be determined by stochastic or unpredictable events, a number of current factors indicate that the re-emergence of clade 2.3.4.4 Gs/GD HPAI viruses in wild birds inhabiting the United States and Canada is plausible and may be probable. First, contrary to the historical (pre-2002) paradigm that HPAI is a poultry-specific disease, there is growing evidence that Gs/GD HPAI viruses are perpetuated in an avian reservoir characterized by bidirectional viral exchange between wild and domestic bird hosts (Bodewes and Kuiken 2018, Lycett et al. 2020). Bidirectional virus exchange appears to be facilitating the adaptation of Gs/GD HPAI viruses in wild bird hosts following introduction from poultry (Kwon et al. 2017, Pantin-Jackwood et al. 2017, van den Brand et al. 2018, Seekings et al. 2021) and promoting viral dispersal via migratory bird movements (Global Consortium for H5N8 and Related Influenza Viruses 2016, Lycett et al. 2020), though poultry production and trade also play a role in viral dissemination. Additionally, the frequency and geographic extent of HPAI occurrences among wild and captive birds have increased since the emergence of Gs/GD HPAI viruses (Figures 2–3) despite concerted global mitigation and control efforts targeted towards domestic poultry. Therefore, recent trends suggest that eradication of Gs/GD HPAI viruses from a global avian reservoir is unlikely to be imminent and that continued outbreaks of HPAI among wild and captive birds should be expected.



East Asia represents an important geographic area where outbreaks of HPAI have repeatedly occurred among wild and captive aquatic birds following the emergence of Gs/GD HPAI viruses (since 2002). Countries in East Asia that have repeatedly been affected by past outbreaks of HPAI in wild birds include Japan, South Korea, and Russia (Marchenko et al. 2011, 2015; Sakoda et al. 2012; Jeong et al. 2014; Baek et al. 2021). These countries provide important breeding, molting, staging, or wintering habitat for numerous species of waterfowl, shorebirds, and gulls that inhabit North America at other times of year including: dunlin (*Calidris alpina*; Winker and Gibson 2010, Gill et al. 2013), emperor goose (*Anser canagicus*; Hupp et al. 2007, Ramey et al. 2019), glaucous gull (*Larus hyperboreus*; Ahlstrom et al. 2021), king eider (*Somateria spectabilis*; Phillips et al. 2006), long-tailed duck (*Clangula hyemalis*; Petersen et al. 2003), northern pintail (*Anas acuta*; Miller et al. 2005, Flint et al. 2009), sharp-tailed sandpiper (*Calidris acuminata*; Handel and Gill 2010), and Steller's eider (*Polysticta stelleri*; Dau et al. 2000). Consequently, there is evidence for ongoing bidirectional dispersal of AI viruses by migratory birds between East Asia and North America via Alaska (Ramey et al. 2015, 2018b; Jeong et al. 2019). This is the same pathway as purported to have led to the previous introduction of Gs/GD HPAI viruses into the United States and Canada in 2014 (Lee et al. 2015, Ramey et al. 2016, Hill et al. 2017). Therefore, additional incursions of AI viruses from East Asia to North America via this pathway should be expected.

Europe also represents a region where HPAI outbreaks in wild birds have become increasingly widespread (Verhagen et al. 2021; Figure 3). Prior research indicates bidirectional viral dispersal between Europe and North America via the North Atlantic (Wille et al. 2011, Hall et al. 2014, Huang et al. 2014). The specific taxa purportedly involved in AI virus dispersal via this trans-Atlantic pathway and the frequency of introduction events have generally been less well-described as compared to the North Pacific Basin. As a result, the likelihood for future introductions of HPAI viruses from Europe into North America by wild birds remains unclear.

Should future incursions of Gs/GD HPAI viruses from East Asia or Europe into North America via wild birds occur, the economic, ecological, and cultural ramifications could be considerable. For example, the economic consequences of prior wild bird-mediated introductions to the poultry industries in the United States and Canada resulted in damages estimated at several billion United States dollars, suggesting that costs of future outbreaks could be comparable (Greene 2015, Hagerman and Marsh 2016). Large-scale mortality events affecting thousands of wild birds, such as those that have previously occurred in East Asia and Europe (Chen et al. 2006, Kleyheeg et al. 2017), could have detrimental effects to specific populations of North American wild bird species, particularly those that are threatened or endangered. Large-scale mortality events could also affect participation in culturally and economically important human uses of wildlife such as subsistence hunting of Indigenous peoples (Charania et al. 2014) and sport hunting among a broader public (Dishman et al. 2010). Future introductions of Gs/GD HPAI could also result in human illness or mortality, particularly if viruses are able to evade biosecurity and enter poultry production systems given a precedent for viral exposure via infected domestic birds (Van Kerkhove et al. 2011).

Important data gaps obscure our ability to forecast future introductions of Gs/GD HPAI viruses from East Asia or Europe into North America and the consequences thereof. For example, the geographic extent and host species in which Gs/GD HPAI viruses are enzootic remain enigmatic despite previous and ongoing research and surveillance efforts. This is, in part, a function of inconsistent sampling across space and time and the evolution and adaptation of Gs/GD HPAI viruses among wild and domestic maintenance hosts comprising the global avian reservoir. Additionally, the persistence of Gs/GD HPAI viruses in the environment is poorly understood despite the recognition that this mechanism likely plays some role in recurrent epidemics among wild birds (Brebán et al. 2009). Though information is limited, previous laboratory and field experiments provide support that AI viruses, including Gs/GD HPAI viruses, may remain infectious for periods of weeks or months within environmental surface waters (Brown et al. 2007, Keeler et al. 2014, Ramey et al. 2020). Also, our understanding of how population immunity may influence the establishment of Gs/GD HPAI viruses in wild bird populations is incomplete. Laboratory experiments provide evidence that the immune status of birds, as influenced by prior infection with endemic AI viruses, influence the probability of viral transmission (Latorre-Margalef et al. 2017, Segovia et al. 2018); however, it is unclear how such heterotypic immunity (priority acquired immunity to different AI viruses) influences the establishment of



introduced AI viruses in North America. Furthermore, surveillance information regarding AI viruses maintained among wild birds inhabiting areas directly adjacent to North America, such as Far Eastern Russia (e.g., Kamchatka and Chukotka) and Greenland, have been extremely limited through both space and time (Hjulsager et al. 2012, Sivay et al. 2012, Hartby et al. 2016, Gaidet et al. 2018). Thus, information on viral threats occurring in wildlife at areas most spatially proximate to North America remain cryptic. Information on the timing, frequency, and routes of intercontinental migratory movements across the North Atlantic and North Pacific Basins is still incomplete for numerous wild bird hosts of AI viruses that may be capable of dispersing viruses from Europe or Asia into North America. This includes previously mentioned taxa for which existing data only reflects birds from specific age and sex classes, a relatively small number of marking sites, or a limited portion of the annual cycle. As a result, our ability to quantify wild bird-mediated viral dispersal is constrained by a relatively coarse understanding of routes and timing of migratory movements between North America and adjacent regions. Finally, our understanding of the susceptibility of North American wildlife species to disease on account of infection with Gs/GD HPAI viruses is limited to information for a relatively small number of individuals and species infected with a narrow range of genetic viral variants as assessed through field observation (Ip et al. 2016) and experimental challenge studies (Brown et al. 2006, Pasick et al. 2007, Hall et al. 2009, Spackman et al. 2017, Luczo et al. 2020).

PREPARING FOR FUTURE OUTBREAKS OF HPAI IN WILD BIRDS

Until late November 2014, HPAI outbreaks in the United States and Canada were restricted to poultry and stringent biosecurity for domestic bird production, in conjunction with prompt depopulation of affected or potentially exposed poultry flocks, was sufficient for eradicating this economically important avian disease. Even during 2014–2015, this strategy was ultimately successful in eradicating HPAI in domestic poultry in the United States and Canada, albeit at significant economic cost; however, the apparent evolving role of wild birds in the maintenance and dispersal of clade 2.3.4.4 Gs/GD HPAI viruses suggests that this strategy alone may not be sufficient for limiting damages moving forward. Thus, managers of wildlife and their habitats may consider the development or adoption of mitigation strategies if future losses from HPAI outbreaks, including diseased birds and economic losses, are to be minimized.

In North America, the management of wildlife resources and their associated habitats is the responsibility of diverse local, state, provincial, territorial, tribal, and federal agencies and Indigenous organizations with different policies and mandates. Therefore, specific management strategies are not applicable or appropriate in all instances. As such, wildlife management agencies may consider 3 simple guiding principles in the consideration, development, and implementation of strategies tailored to organizational priorities and mandates that aim to mitigate direct and indirect damages of HPAI to wildlife resources. Specifically, managers and organizational units may work within their respective chains of command and with wildlife health offices, as applicable, to be informed, be prepared, and take action as appropriate for their respective agency or organization. Some organizations may already be applying these principles in existing response and management plans.

Be informed

As a first step towards the potential development and application of management actions to mitigate damages incurred through the dissemination of HPAI via wild birds, managers and organizational units may choose to be informed. Many state, provincial, territorial, federal, and tribal wildlife management agencies and Indigenous organizations maintain some level of wildlife health expertise to provide assistance with the investigation of wildlife morbidity and mortality events and conduct disease surveillance. In some cases, organizations without these resources have established partnerships or agreements with outside agencies and laboratories to provide the

necessary support in the event of an outbreak. In either scenario, these existing support networks serve as an initial place to seek information from wildlife health experts to help guide planning for and response to HPAI outbreak events.

For those managers or organizational units lacking such support networks or for those seeking additional information, rigorous scientific summaries on the occurrence and ecology of AI viruses in wild birds are widely available through a variety of sources (Table 1). For example, situational updates and summary reports on AI viruses in wild birds can be accessed through organizational websites including those for the Food and Agriculture Organization of the United Nations, OIE, the Canadian Wildlife Health Cooperative, the United States Department of Agriculture, and the United States Geological Survey (Table 1). Alerts and reports are also sporadically issued by the United States Interagency Steering Committee for Surveillance for Highly Pathogenic Avian Influenza in Wild Birds, the United States Geological Survey National Wildlife Health Center, and the International Society for Infectious Diseases (Table 1). The latter organization offers a publicly available subscription service (ProMED) that provides frequent global updates on infectious disease outbreaks, including highly pathogenic avian influenza in wild birds (Table 1). Another source of potentially useful contemporary information is recent review articles that offer synthesis of the dynamic trends of HPAI infection in wild birds. Recent review products have been published on the changing role of wild birds in the epidemiology of AI viruses (Bodewes and Kuiken 2018), the evolution and global spread of clade 2.3.4.4 Gs/GD HPAI viruses (Lee et al. 2017a), ongoing challenges with Gs/GD HPAI in domestic and wild birds in Europe (Verhagen et al. 2021), and lessons learned from research and surveillance directed towards HPAI viruses in wild birds inhabiting North America (Ramey et al. 2018a). Reading recently published reports is another way to obtain valuable information towards the development of science-based management strategies. Example topics that are relevant towards the consideration and development of mitigation strategies for HPAI in North American wildlife include the susceptibility of common wild and peridomestic bird species to infection and clinical disease when exposed to clade 2.3.4.4 Gs/GD HPAI viruses (Pantin-Jackwood et al. 2016, Spackman et al. 2017, Kwon et al. 2018, Bosco-Lauth et al. 2019, Shearn-Bochsler et al. 2019, Luczo et al. 2020)

TABLE 1 Useful websites for obtaining information and updates on highly pathogenic avian influenza in wild birds and use of personal protection equipment in investigations thereof

Organization	Url
Food and Agriculture Organization of the United Nations	http://www.fao.org/ag/againfo/programmes/en/empres/Global_AIV_Zoonotic_Update/situation_update.html
World Organisation of Animal Health	https://www.oie.int/en/disease/avian-influenza/
Canadian Wildlife Health Cooperative	http://www.cwhc-rcsf.ca/avian_influenza.php
U.S. Department of Agriculture	https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/animal-disease-information/avian/avian-influenza/ai
U.S. Geological Survey	https://www.usgs.gov/ecosystems/fish-wildlife-disease/wildlife-diseases-and-agriculture/avian-influenza
U.S. Geological Survey National Wildlife Health Center	https://www.usgs.gov/centers/nwhc/science/avian-influenza
International Society for Infectious Diseases (ProMED)	https://promedmail.org/
Occupational Safety and Health Administration	https://www.osha.gov/avian-flu
Department of the Interior	https://pubs.er.usgs.gov/publication/tm15C2
Centers for Disease Control and Prevention	https://www.cdc.gov/flu/avianflu/groups.htm



and the persistence of infectious AI viruses in surface waters of North American wetlands (Keeler et al. 2014, Ramey et al. 2021). Other topics relevant to specific management areas include the current distribution, abundance, movement patterns, and interaction of susceptible wildlife species with domestic species in or near management areas, and understanding past outbreaks or susceptibility of infection in wildlife species that occur within a management area.

By reviewing and interpreting the scientific data on the occurrence and ecology of AI viruses in wild bird hosts through information sources, including those outlined here, wildlife managers, organizational units, and agencies within North America will be able to better assess what, if any, preparations and potential mitigation actions are appropriate for their organization and management unit. Agency and organizational personnel would benefit from being informed on the current global situation regarding Gs/GD HPAI in wild birds to make decisions to improve outbreak preparedness, participate in effective surveillance programs, contribute to research filling critical information gaps, and respond to outbreak events in wildlife through targeted actions and communications.

Be prepared

A second possible step towards determining whether and how to develop and apply management actions to mitigate damages incurred through the dissemination of HPAI via wild birds is to be prepared. Preparations include numerous elements such as coordination and communication within a management organization and with external agricultural and public health agency partners, consideration of the appropriate use of personal protective equipment (PPE) during outbreak events, determining whether and how to document the geographic extent of HPAI outbreaks in wild birds, evaluation of management options to mitigate the dissemination or impacts of HPAI viruses, and elevating situational awareness as determined to be appropriate. Managers, organizational units, or agencies may choose to develop specific plans or decision trees in advance to guide decisions and actions (or non-actions) given the detection of HPAI in North American wild birds.

Given that the occurrence of Gs/GD HPAI viruses in wild birds inhabiting North America presents some level of health risk among wild and domestic animals and the humans that interact with them, communication among wildlife, agricultural, and public health management agencies and organizations is critical to fostering effective coordination (Sleeman et al. 2017). This coordination among wildlife management, agricultural, and public health agencies working on HPAI helps to ensure that local, state, provincial, territorial, tribal, Indigenous, and federal points of contact are up to date; organizational expertise is identified; responsibilities are assigned to key personnel; communication and surveillance plans are established and maintained; and management actions (or non-actions) are identified and agreed upon before HPAI outbreaks occur in wild birds inhabiting North America.

Internal communications (those shared within a wildlife management agency or organization) and external communications (those shared with other agencies, organizations, stakeholders, and the public) may be most effective when conducted by professional external affairs or public information experts and when initiated both prior to and early in the course of an outbreak event (Reynolds et al. 2014). Communication products can be developed prior to an outbreak and include joint agency talking points, pre-approved fact sheets, press releases, website information, social media posts, and informational brochures. Topics of these communications may include details on signs of disease in wild birds, how to report sightings of sick birds, the management responses that could be necessary, and the potential health risks for wild birds, domestic animals, and humans.

Another important component of organizational preparation is to determine whether and how to provide guidance regarding the use of PPE during an outbreak to field personnel and the public. Previous research indicates that human infection with wild bird-origin AI viruses may be a relatively low probability event (Gill et al. 2006) but also one with potentially high consequences when considering Gs/GD HPAI viruses (Gilsdorf et al. 2006). Thus, agencies may choose to critically assess what constitutes appropriate PPE given perceived risk, if such equipment is



currently available or can be readily acquired, and whether personnel are properly trained in appropriate and effective use. Guidance for personnel investigating a potential avian influenza mortality event is available from the Occupational Safety and Health Administration, the Department of the Interior, and the Centers for Disease Control and Prevention (Table 1). A previous rapid risk assessment for SARS-CoV-2 may also provide helpful insight as to how inter-jurisdictional and inter-organizational efforts to assess risk helps with guidance regarding the use of PPE during an outbreak scenario (Runge et al. 2020).

Another important component of preparedness planning is to determine whether and how to document the geographic extent of HPAI outbreaks in wild birds (Preece et al. 2017). This may include quantifying the number or proportion of birds exhibiting disease or mortality, effects of disease on local bird populations, and observational effort. This hazard characterization step is critical to evaluating whether HPAI threatens North American wildlife beyond small-scale mortality events and for the early detection of changes in the level of risk to animal health. Efforts to thoroughly characterize and document wild bird mortality events may also be useful towards bolstering ongoing interagency HPAI passive surveillance efforts. Determining whether and how to document the geographic extent of HPAI outbreaks in wild birds represents a good example action for which prior intra- and inter-organizational coordination and communication may be important for promoting the efficient and effective collection of useful information.

Preparedness planning of specific management actions to mitigate the risk of viral spread among birds, from birds to other wildlife, and from birds to other potential hosts (e.g., domestic animals, companion animals, humans) is a challenging task given currently available information but an area that also warrants careful consideration. There is considerable, albeit incomplete, data to guide decisions regarding whether and how to pursue mitigation actions during an outbreak event. Example actions might include the suspension of banding or capture efforts during outbreaks, particularly those that use bait and promote the concentration of wildlife, which may facilitate increased viral prevalence (Soos et al. 2012); the restriction of public access to affected wetlands to limit human exposure and spread via fomites (virally contaminated inanimate objects such as boots, waders, or vehicles) given that Gs/GD HPAI viruses may remain infectious in water for extended periods (Brown et al. 2007, Domanska-Blicharz et al. 2010); the development and implementation of disinfection protocols for vehicles, boats, and gear used to access potentially affected sites to minimize viral dissemination through human activities (Dargatz et al. 2016); the suspension of hunting in potentially affected areas or species to limit possible human exposure and spread via virally contaminated bird carcasses or fomites (Gill et al. 2006, Gilsdorf et al. 2006); and the manipulation of water levels of small managed wetlands to facilitate faster viral inactivation (e.g., through increasing ultraviolet penetration or raising the water temperature; Sagripanti and Lytle 2007, Weber and Stilianakis 2008). Ideally, if managers or agencies decide to implement management actions during an outbreak aimed at mitigating negative consequences to animal or human health, they would be developed and applied in such a manner as to facilitate subsequent evaluation of efficacy.

Perhaps one of the most important components of preparing for potential HPAI outbreaks in North American wildlife is for managers and agencies to consider elevating their situational awareness (e.g., to be vigilant) regarding this important animal disease. For decades, the successful eradication of HPAI in domestic poultry in the United States and Canada has been dependent on early disease detection and a prompt response. Therefore, a similar approach may also be effective for facilitating mitigation actions in wild birds or their habitats. The vigilance of wildlife managers is important to early detection capabilities within wild bird populations of the United States and Canada, and the prompt detection of any future incursions of the Gs/GD HPAI viruses into North America may help reduce the risk of cross-species transmission to poultry. Given that Gs/GD HPAI has previously been detected through the investigation of morbidity and mortality in North American waterfowl and other wild birds (Ip et al. 2016, Shearn-Bochsler et al. 2019), prompt reporting of avian health issues or suspect mortality cases may ultimately inform effective response and mitigation activities in wild and domestic animal sectors. Organizational units and agencies may obtain useful information from within existing support networks (as applicable) to understand what is considered normal or baseline wild bird mortality and specific trigger points or thresholds for sick, diseased, or dead birds on managed lands that may signify abnormalities and lead to the initiation of an outbreak investigation.



Take action (as appropriate)

A final potential step towards determining whether and how to apply management actions to mitigate damages incurred through HPAI outbreaks in wild birds is to take appropriate action, or to choose inaction, per information obtained and plans developed specifically for an organization or management unit. Potential actions include those outlined previously and the participation in or support of research and surveillance programs. Numerous agencies and academic institutions within the United States and Canada conduct limited active surveillance for HPAI in wild birds or have research programs to better understand the maintenance and dispersal of AI viruses. Representatives from these agencies and institutions often request assistance for active surveillance efforts from wildlife managers or organizational units in the form of help with field logistics or biological sampling of hunter-harvested or live wild birds for AI viruses. Passive surveillance is another important component of early detection and response (Ip et al. 2016). Wildlife managers may find it helpful to communicate within their organization and interagency network to (re-) familiarize themselves with the submission processes for HPAI-suspect bird carcasses at the Canadian Wildlife Health Cooperative, the United States Geological Survey National Wildlife Health Center, the University of Georgia Southeastern Cooperative Wildlife Disease Study, or their local, state, provincial, territorial, or federal diagnostic laboratory or wildlife agency prior to the onset of migratory periods for wild birds. Finally, though this review has focused on the introduction of Gs/GD HPAI viruses to North American wildlife via wild bird migration, the importation of exotic wildlife to the United States and Canada represents another plausible route of viral dissemination (Suetens et al. 2004). Therefore, the United States Fish and Wildlife Service is laying the groundwork for testing illegal wildlife imports for high consequence diseases including HPAI. It is expected that additional information on this program will become available as it is established.

MANAGEMENT IMPLICATIONS

Given the apparent increasing frequency of outbreaks of HPAI among wild birds globally, including ongoing outbreaks of HPAI in Europe and Asia and the prior introduction of Gs/GD HPAI viruses into the United States and Canada, wildlife managers and agencies in North America may consider raising their situational awareness regarding this important emergent wildlife disease. Furthermore, managers, organizational units, and management agencies within North America may choose to be informed, be prepared, and take action, as appropriate, to limit impacts of HPAI to wildlife resources and the stakeholders that rely upon them.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

No animals were handled, observed, or otherwise potentially disturbed in the preparation of this review product.



DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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