The Changing Dynamics of Highly Pathogenic Avian Influenza H5N1: Next Steps for Management & Science in North America

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ABSTRACT

Highly pathogenic avian influenza virus (HPAIV) H5N1 was introduced in North America in late 2021 through trans-Atlantic and trans-Pacific pathways via migratory birds. These introductions have resulted in an unprecedented and widespread epizootic event for North America, heavily affecting poultry and free-living wild birds in the spring and summer of 2022. The North American incursions are occurring in the context of Europe's largest epidemic season (2021 – 2022) where HPAIV may now be enzootic. A continued North American epizootic is expected in the fall of 2022 as migratory waterfowl return from their breeding grounds. The magnitude of the North American HPAIV spread indicates the need for effective decision framing to prioritize ongoing management needs and scientific inquiry, particularly for species at risk and interface areas for wildlife, poultry, and humans. The challenges of this global One Health disease could benefit from a decision framing which may result in improved collaboration across stakeholders, identification of management options, and prioritization of scientific needs. Here, we provide an overview of the Eurasian origin HPAIV H5N1 introduction, including a shift in the dynamics of disease, which has resulted in severe disease in wild birds. It is unclear if wild bird may have been previously not exposed or asymptomatic to disease. We seek to bring attention to the detrimental effects this One Health issue may have on wild birds, poultry, and potentially human health and to suggest that reframing ongoing disease management as decisions, rather than as scientific endeavors, could be a valuable change in focus.

Keywords: structured decision making; avian influenza; disease management; H5N1 clade 2.3.4.4b; wild birds; poultry

INTRODUCTION

In 2021 and 2022, unprecedented outbreaks of highly pathogenic avian influenza virus (HPAIV) have resulted in a large number of detections and mass mortalities in wild birds as well as effects on domestic poultry across Europe, parts of Asia, Africa and now North America (CMS & FAO 2022). In late 2021, North America began to experience what may be its largest and most deadly incursion of H5 HPAIV to date, with a range of signs across wild bird species from generally asymptomatic infections in dabbling ducks to large scale die-offs in colonial nesting or gregarious birds such as northern gannets *(Morus bassanus)* and black vultures *(Coragyps atratus)* ("WHISPers" 2022). As part of the current outbreak, Eurasian-origin H5N1, belonging to the clade 2.3.4.4b viruses, was first detected in Newfoundland, Canada, in captive poultry at an exhibition farm in December of 2021 and retrospectively in a free-living great black-backed gull *(Larus marinus)* in late November 2021 (Caliendo et al. 2022). By January 2022, H5N1 was detected in North and South Carolina in the United States (Bevins et al. 2022). Since the re-introduction of this viral lineage into North America, it has rapidly spread across 45 of the continental United States (USDA APHIS 2022a) and all Canadian provinces and territories except for the Northwest Territories ("National Avian Influenza - Wild Positives" 2022). As of October 2022, there have been 32 wild bird mass mortality events (MME) reported (individuals affected: > 75, range 75-3,000) in the United States. There have been ~14,600 confirmed H5N1 wild bird mortalities ("WHISPers" 2022) and over 47 million domestic poultry have been infected or culled in the United States (USDA APHIS 2022b). While endemicity of HPAIV has already occurred in Asia, Africa, and most recently Europe (Pohlmann et al. 2022), in North America the degree of unknown asymptomatic infection in wild birds and migratory species is of great concern because it may result in increased virus fitness and dissemination. High levels of uncertainty remain in what future highly pathogenic avian influenza disease dynamics will look like in North America, particularly given the widespread geographic range and number of free-living species affected. This uncertainty confounds disease management responses.

Large-scale animal disease response and management is challenging for a variety of reasons, including complicated and uncertain disease dynamic, diverse groups of authorities (e.g., local, state, tribal, and federal agencies; transnational authorities; and non-governmental research groups) and stakeholders (e.g., human health, wildlife, poultry), and limited resources. Where resources and capacity exist for implementation, more standardized disease management recommendations exist for domesticated poultry ("Chapter 10.4 Infection with high pathogenicity avian influenza viruses" 2021) as provided by the World Organization for Animal Health (WOAH). HPAIV priorities for the industry are to reduce transmission to and within domestic poultry by improving biosecurity measures and wildlife deterrence practices, which also reduces the incidence of spillback (i.e., transmission from poultry back to wildlife). No suite of organized management actions currently exists, however, to respond to HPAIV in wild birds. A cohesive One Health approach could address disease management response and help reduce future negative HPAIV effects.

In this paper, we argue that a shift in focus towards decision making could provide a valuable framework to guide the joint and collaborative work of management agencies and scientists, for the benefit of wild bird conservation and agricultural production. The complexity of migratory bird conservation and poultry production (e.g., scale complexity, governance structures, limited resource availability), coupled with the high degree of biological uncertainty of the changing disease dynamics makes the formulation and execution of management decisions in the face of

HPAIV extremely challenging with no precedent. We suggest that formal methods of decision analysis can aid in framing decisions, allocating scarce resources, and identifying the prioritization of scientific inquiry to inform management and conservation actions.

AVIAN INFLUENZA ORIGIN AND EVOLUTION OF CLADE 2.3.4.4 H5NX HPAIV

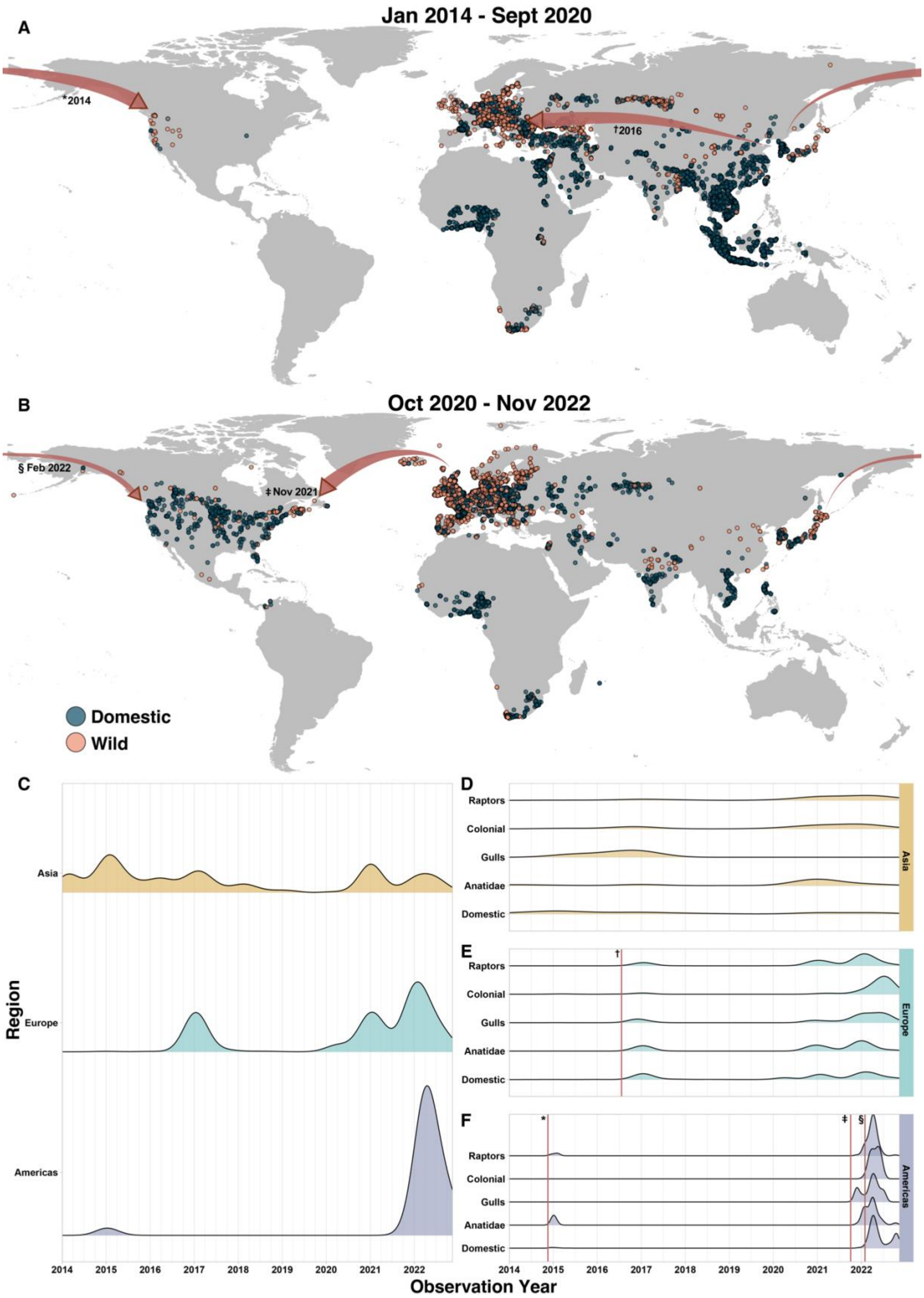
Avian influenza viruses (AIV) belong to the influenza A viruses (family: Orthomyxoviridae; genus: *Orthomyxovirus*), which are enveloped viruses of negative-stranded RNA with eight gene segments that may also infect a diversity of vertebrate hosts including birds and mammals, including humans. Currently, 16 hemagglutinin (HA) and 9 neuraminidase (NA) antigenic subtypes have been found in birds, and these combinations are used to characterize AIVs into subtypes (e.g., H5N1, H7N8) (Webster et al. 1992). Phenotypically, AIV's are often described based on their pathogenicity in chickens: highly pathogenicity avian influenza viruses (HPAIV), historically termed fowl plague, cause high mortality; low pathogenicity avian influenza viruses (LPAIV) may produce asymptomatic infections or mild to severe respiratory disease often presenting as weight loss and a drop in or loss of egg production in poultry (Suarez, 2008). Most HA subtypes result in LPAIV, with only H5 and H7 currently known to have HPAIV strains.

Historically, HPAIV infections occurred in domestic poultry and did not circulate in wild birds, except for an isolated large outbreak in common terns (*Sterna hirundo*) in South Africa in 1961 (Rowan 1962; Becker 1966). Wild birds began to be affected by HPAIV beginning with the highly pathogenic H5N1 virus lineage A/Goose/Guangdong/1/96 (Gs/GD), which was first isolated in a domestic goose in China in 1996 (Xu et al. 1999). Increased diversification of Gs/GD via mutations and repeated reassortments with common and globally distributed LPAIV subtypes has resulted in maintenance of descendant Gs/GD viral lineages. Since its emergence, Gs/GD descendants have demonstrated an aptness to reassort into new genome constellations (H5Nx, with different NA subtypes) (de Vries et al. 2015). The HA gene of H5 viruses have been divided into monophyletic clades (zero to nine) (WHO/OIE/FAO H5N1 Evolution Working Group 2008). Clade 2.3 caused infections in birds and human throughout Asia from 2003-2008 (Neumann et al. 2010). Clade 2.3.4, originally isolated in China in 2005, continued to reassort (de Vries et al. 2015). Viral clade 2.3.4.4 emerged in Asia in 2013 and resulted in an increased circulation via wild birds and notably an improved adaptation to infect wild waterfowl (i.e., asymptomatic infection and high shedding rates for certain species) (Kang et al. 2015; Lee et al. 2017). Viral clade 2.3.4.4 has been further divided into eight subclades (2.3.4.4a – 2.3.4.4h) (Li et al. 2020). Notably, clade 2.3.4.4b, which emerged in China in 2013, has resulted in a broadened geographic spread into Asia, the Middle East, Africa, and Europe, and increased numbers of outbreaks since 2016 (Cui et al. 2022). The descendant viruses from Gs/Gd belonging to clade 2.3.4.4b have been associated with increased deaths and transcontinental spread to over 80 countries causing outbreaks and continued circulation in domestic poultry and increasingly in wild birds (Lee et al. 2017; Caliendo et al. 2022; Pohlmann et al. 2022) and to a lesser extent resulting in incidental and non-transmissible mammal and human infections (World Health Organization 2022).

Conventionally, aquatic birds of the Anseriformes (ducks, geese, and swans, here-after termed waterfowl) and Charadriiformes (gulls, terns, and shore birds) are natural reservoirs for avian influenza viruses (Webster et al. 1992; Olsen et al. 2006). Waterfowl and other aquatic species have commonly been asymptomatic carriers of LPAIV, presenting with mild enteric infections, which circulate among wild birds. Transmission of LPAIVs primarily occurs via an indirect fecal-oral route involving an environmental exposure, which provides opportunity for spread via shared waterbodies along migratory routes or wintering areas of congregation (Fouchier & Munster 2009; Ramey et al. 2020; Ahrens et al. 2022). The Gs/GD H5Nx viruses, however, have also evolved to replicate within the respiratory tract and can thus transmit directly through a respiratory route (i.e., respiratory droplets). Historically, HPAIV outbreaks in poultry have almost exclusively resulted from spillover of LPAIV from wild aquatic birds (Swayne & Suarez 2000) into poultry where the viruses mutate to HPAIV (Suarez, 2008)., The dynamics of the current HPAIV outbreak differ from this historical pattern, however, as wild birds are being impacted at an inordinate rate with wild birds now transmitting HPAIV (Pohlmann et al. 2022; Ramey et al. 2022).

SPREAD OF HPAIV CLADE 2.3.4.4 AND INCREASING DISEASE IN WILD BIRDS

North America’s first H5 HPAIV outbreak to extend beyond poultry and also affect wild birds was caused by H5 viruses belonging to clade 2.3.4.4 in 2014/2015 with dispersal of H5N8 via migratory birds moving from Asia to the Pacific Flyway then spreading to the Central and Mississippi Flyways (Fig. 1A) (Ip et al. 2015; Lee et al. 2015; Bevins et al. 2016; Ramey et al. 2016). Eurasian H5 viruses descended from Gs/GD had not been detected in North America prior to 2014. Over 50 million domestic poultry were affected across 15 US states (Ramos et al. 2017), and wild birds were affected in 13 US states (Animal and Plant Health Inspection Service et al. 2016; Bevins et al. 2016). Some short-term circulation and viral persistence occurred until 2016, but H5 was successfully eradicated from poultry circulation via culling control measures and was rarely detected in wild birds indicating minimal circulation. HPAIV was not detected in wild birds in North America again until the winter of 2021 in the province of Newfoundland, Canada (Caliendo et al. 2022). Genetic analysis of the Newfoundland detection suggests the transatlantic spread into North America likely occurred via migration from Northwestern Europe via Iceland, Greenland, or pelagic routes (Fig. 1B) (Bevins et al. 2022; Caliendo et al. 2022), the opposite side of the continent from the 2014/15 incursion. However, a separate transpacific incursion was detected infecting a bald eagle (*Haliaeetus leucocephalus*) recovered from British Columbia, Canada in early 2022 whose viral lineage was found to be most closely genetically similar to a white-tailed eagle (*Haliaeetus albicilla*) from Hokkaido, Japan (Alkie et al. 2022). Additional detections of the Hokkaido origin lineage in North America have not yet been reported. Since the initial detections in Newfoundland, H5N1 has spread throughout most of Canada and the continental United States and most recently (late October – November, 2022) has been detected in both poultry and wild birds in Mexico and expanding to South America in Colombia (EMPRES 2022; Fig 1B).


A
Jan 2014 - Sept 2020
*2014
†2016
B
Oct 2020 - Nov 2022
§ Feb 2022
‡ Nov 2021
Domestic
Wild
C
Asia
Europe
Americas
Region
D
Raptors
Colonial
Gulls
Anatidae
Domestic
Asia
E
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Raptors
Colonial
Gulls
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Europe
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Raptors
Colonial
Gulls
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2014
2015
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2017
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2022
Observation Year

Fig. 1) **Spread of Clade 2.3.4.4b in domestic and wild birds.** A-B) Map of HPAIV detections in domestic (blue circles) and wild (coral circles) birds from A) January 2014 – September 2020 with red arrows demonstrating the incursion from Asia to North America in 2014 (* symbol), and incursion from Asia to Europe in 2016 († symbol); B) October 2020 to November 15, 2022 with a red arrows demonstrating the transatlantic incursion from Europe to North America in November of 2021(‡ symbol), and incursion from Japan to British Columbia (§ symbol). C-F) Ridgeline plots, created using the ggridges package (Claus O. Wilke 2022) in R v.4.1.0, of C) the combined wild and domestic bird HPAIV detections across Asia, Europe, and North America; D-F) detections from January 2014 – September 2020 for raptors, colonially nesting species, gulls, wild species within the taxonomic family of Anatidae, and domestic birds scaled across D) Asia; E) Europe, with † symbol indicating timing of incursion of from Asia in 2016; and F) N. America, with the * symbol indicating the incursion from Asia in 2014, the ‡ symbol indicating the incursion from Europe in 2021, and the § symbol indicating the incursion from Japan in early 2022. Maps and all plots are simplified by representing only H5N8 and H5N1 confirmed detections in birds, domestic and wild, from 2014 to 2022 from the Emergency Prevention System for Animal Health (EMPRES) of the Food and Agriculture Organization of the United Nations.

CHANGING HPAIV DYNAMICS

With the emergence of the current Eurasian origin H5N1, the dynamics of HPAIV have changed in two important ways: symptomatic infections widely circulating in wild birds; and a distinct shift in seasonality of disease. Prior to the December 2021 North American HPAIV incursion, Europe experienced repeated incursions, occurring from 2005-2020, with outbreaks, or increases in disease prevalence, increasingly affecting wild birds and poultry (Verhagen et al. 2021). Notably, the 2016 incursion of clade 2.3.4.4b in Europe, ultimately dominated by the H5N8 circulating strain, resulted in an increase in number of affected wild birds (Figs. 1A; 1E). The current European outbreak is now dominated by clade 2.3.4.4b H5N1, which has resulted in the largest European HPAIV season (2021-2022) thus far (Pohlmann et al. 2022). H5N1 infections were detected in a broader range of wild birds, including terrestrial species and colonially nesting seabirds that had previously been much less affected or species with novel infections (Figs. 1C; 1D-F) (European Food Safety Authority et al. 2022a). Prior to 2021-2022, European HPAIV outbreaks followed a cycle of high intensity outbreaks in the fall/winter and sharp declines in the summer (European Food Safety Authority et al. 2022b; Pohlmann et al. 2022). However, changes in seasonality dynamics were seen in Europe in the summer of 2021 with increased detections in spring/summer including several large-scale MMEs in colonially nesting birds (European Food Safety Authority et al. 2022b).

Compared to historical patterns, North American wild bird mortality due to HPAIV has been much higher than expected during the typically low AIV transmission periods of spring and summer of 2022 (Pohlmann et al. 2022). A similar temporal pattern of higher than expected transmission and outbreaks was also seen in Europe during summer 2022 (European Food Safety Authority et al. 2022b). We recognize that different evolutionary dynamics are exhibited by different AIV lineages (Hill et al. 2022). For example, transmission and infection dynamics of HPAIV viral clades prior to 2.3.4 resulted in limited spread due to reduced host movement and reduced host range (Antigua et al. 2019). Unfortunately, there has been a shift in the range and distribution of affected species beginning with clade 2.3.4 and increasing with clade 2.3.4.4 (Antigua et al. 2019).

Asymptomatic infections may have increased undetected dissemination and dispersal of HPAIV via long-distance migrants, such as seabirds, shorebirds, waterfowl, and gulls, as symptomatic birds are less likely to successfully migrate long distances (Fig. 1D-F). A recent study predicted that different taxonomic groups contribute to the spread of HPAIV at different rates, with gulls and swans exhibiting the highest rates of H5 viral diffusion as compared to terrestrial or domestic species (Hill et al. 2022). Furthermore, asymptomatic infections can result in increased circulating viruses, which may result in reassortment events and changing viral fitness as previously seen with the evolution of the Gs/GD viral lineages.

CURRENT NORTH AMERICAN HPAIV OUTBREAK AND WILD BIRD IMPACTS

In North America, the current HPAIV outbreak has resulted in a rapid geographic spread (Fig. 2) and affected a diversity of wild birds. Wild waterfowl, seabirds, a variety of wetland birds, and shorebirds, some previously known to be reservoirs and asymptomatic carriers of LPAIV, are susceptible to HPAIV, resulting in mortalities and asymptomatic infections across all groups. Since 2021, increased HPAIV MMEs world-wide have occurred, primarily in colonial-nesting species (i.e., large aggregate nest or roost sites of one or more species) where transmission may be increased due to proximity of birds and nest sites or behaviors of birds that may facilitate viral spread, e.g., vultures feeding on HPAI infected carcasses. Large die-offs can impact populations of these species for decades and may contribute to species collapse and further ecosystem damage, particularly given the ongoing declines in North American birds (Ceballos et al. 2017; Rosenberg et al. 2019). Most MMEs (here defined as > 75 birds) in North America have also been in colonially nesting species (Table 1). A number of those colonial nesting populations or species are listed as sensitive and species of concern due to habitat loss and anthropogenic pressures; however, many colony species are data deficient as monitoring of these populations can be difficult (Rosenberg et al. 2019). For example, Caspian terns (*Hydroprogne caspia*) have nesting colonies in the Great Lakes region of North America and are listed as endangered in Wisconsin and threatened in all other Great Lakes US states. It is estimated that 62% of the Caspian tern population in Lake Michigan died of HPAIV in the summer of 2022 (“Bird flu has killed nearly 1,500 threatened caspian terns on Lake Michigan islands” 2022; “WHISPers” 2022). Additionally, thousands of northern gannets (*Morus bassanus),* along with common murres (*Uria aalgae*), razorbills (*Alca torda*), and great black-backed gulls have been reported washing up on coastlines in the Gulf of St. Lawrence region of Canada (Ann 2022). This region is home to the largest breeding colony of northern gannets in North America, and while population levels had been recently increasing (Sauer et al. 2020), the species has historically faced repeated anthropogenic impacts, like DDT contamination, bycatch, and the Deepwater Horizon oil spill (Chardine et al. 2013). Specifically, there are numerous susceptible populations and species of immediate conservation concern (Table 1).

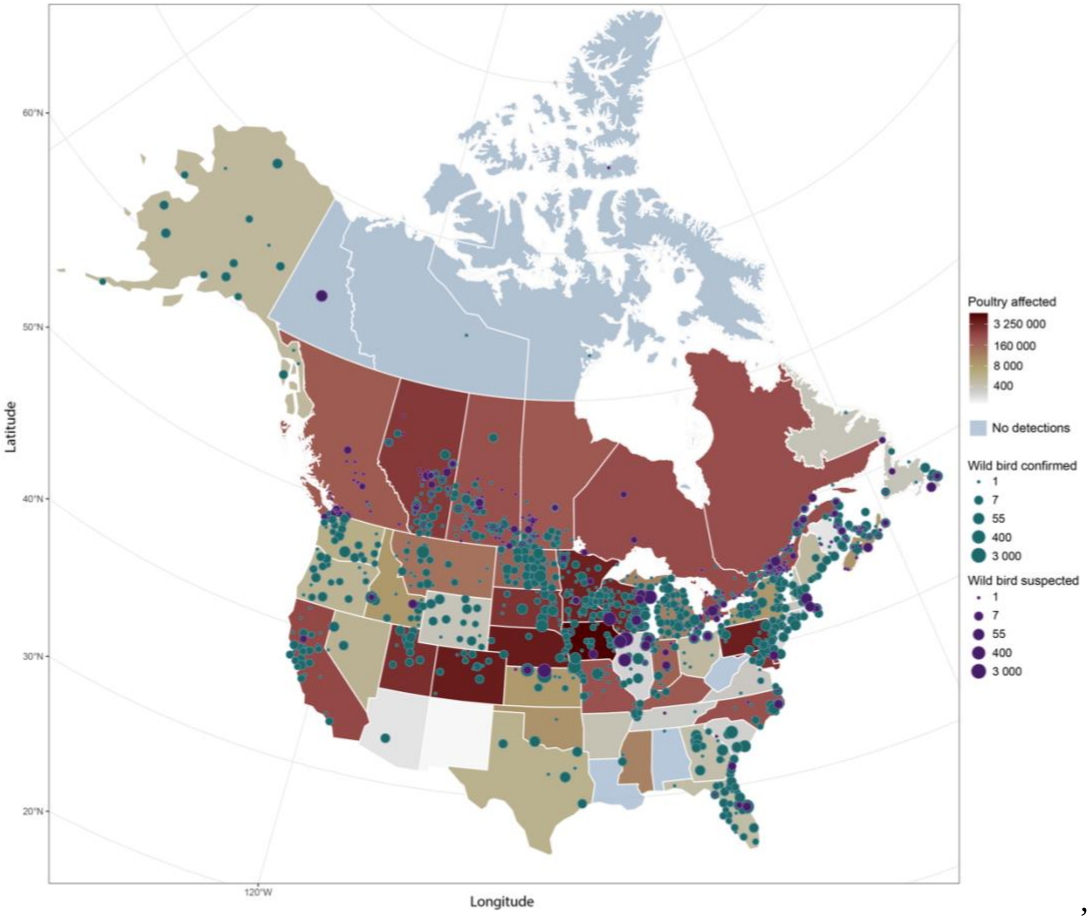

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Fig. 2). Map of the density of poultry (log transformed) affected by HPAIV H5N1from December 2021 to October 2022 across Canadian provinces/territories/US states (Canadian Food Inspection Agency Government of Canada 2022; USDA APHIS 2022b).The darkest red corresponds to the highest number of birds affected and tan/grey corresponds to the lowest number of birds affected. Slate blue indicates no poultry detections were reported for that province/territory/state. Circles (blue = confirmed; purple = suspected) indicate wild bird detections (log transformed) per US county/Canadian census subdivisions (plotted to centroid), circle diameter is scaled by number of detections. Wild bird data collected from USDA and WHISPers (USDA APHIS 2022a; "WHISPers" 2022) current as of October 26, 2022; Canada wild bird data collected from CFIA ("National Avian Influenza - Wild Positives" 2022) current as of October 7, 2022. Base layers downloaded from the United States Census Bureau and the Canada Statistics Agency and are displayed using Lambert canonical projection (Esri: 102009) in R V 4.1.3 and RStudio 2022.02.0.

Table 1. Total number of HPAIV H5 infections reported in North America wild birds with either >75 individuals per species AND/OR is a species that is threatened/listed of conservation concern. Common and species names, taxonomic order, *N* = number of individuals, nesting behavior and non-breeding behavior ([1]Billermn et al. 2022). This list is not meant to be exhaustive but demonstrative of the impacts across colonially nesting birds and species of conservation concern.

Threat level and listing including designations by: [2] BCC = Birds of Conservation Concern 2021 (*Birds of Conservation Concern 2021 Migratory Bird Program* 2021) as continental listed (C) or regionally listed (R); [3]ESA = listed under the USA Endangered Species Act as endangered (E) or threatened (T); [4]SARA = listed under the Canada Species at Risk Act under Schedule 1 (Legislative Services Branch Canada 2022) as endangered (E), threatened (T) or of special concern (SC); US State (ST: State abbrev.) listed as endangered (E) or threatened (T).

Common name	**Species**	**Order**	***N***	**Nesting behavior[1]**	**Non-breeding behavior[1]**	**Threat level/listing**
American coot	*Fulica americana*	Gruiformes	164	Paired solitary	Large flocks, mixed	-
American crow	*Corvus brachyrhynchos*	Passeriformes	146	Cooperative breeder	Communal roost	-
Atlantic puffin	*Fratercula arctica*	Pelecaniformes	5	Colonial	Colonial	ST: ME (T)
Artic tern	*Sterna paradisaea*	Charadriiformes	4	Colonial	Colonial	ST: ME (T)
American white pelican	*Pelecanus erythrorhynchos*	Pelecaniformes	2328	Colonial	Gregarious, flocking	ST: WA (T)
Bald eagle	*Haliaeetus leucocephalus*	Accipitriformes	370	Paired solitary	Social groups	ST: CA, NJ, RI, (E); CT, GA, NC, NM, NY, SC, SD, (T)
Black vulture	*Coragyps atratus*	Accipitriformes	1132	Colonial	Gregarious, communal roosts	-
Canada goose	*Branta canadensis*	Anseriformes	595	Colonial	Gregarious, family groups	-
Caspian tern	*Hydroprogne caspia*	Charadriiformes	1517	Colonial	Large flocks	ST: WI (E); NC, MI (T)
Common eider	*Somateria mollissima*	Anseriformes	137	Often colonial	Large flocks	-
Common tern	*Sterna hirundo*	Charadriiformes	18	Colonial	Colonial	BCC (R)[2]; ST: DE, IL, MD, NC, OH, PA, VT, WI (E); MI, MN, NH, NY (T)

Common name	Species	Order	*N*	Nesting behavior[1]	Non-breeding behavior[1]	Threat level/listing
Double-crested cormorant	*Phalacrocorax auritus*	Pelecaniformes	2761	Colonial	Gregarious	-
Great egret	*Ardea alba*	Pelecaniformes	118	Often colonial	Solitary or flocks	
Great horned owl	*Bubo virginianus*	Strigiformes	222	Solitary	Solitary	-
Herring gull	*Larus argentatus*	Charadriiformes	148	Colonial	Loose groups	-
Horned grebe	*Podiceps auritus*	Podicipediformes	2	Paired solitary	Flocks	SARA (SC)[4]; ST: MN (E)
Lesser scaup	*Aythya affinis*	Anseriformes	1502	Mostly solitary	Large flocks	-
Mallard	*Anas platyrhynchos*	Anseriformes	548	Paired solitary, loose groups	Flocks	-
Northern gannet	*Morus bassanus*	Pelecaniformes	89	Colonial	Small, loose flocks	-
Northern harrier	*Circus hudsonius*	Accipitriformes	2	Paired or polygynous, often loose assemblages	Communal roosts	ST: CT, DE, IA, IL, IN, MO, NH, NJ, OH, RI (E); KY, MA, NY, PA (T)
Osprey	*Pandion haliaetus*	Accipitriformes	3	Paired solitary	Solitary	ST: IL (E); NJ, SD (T)
Peregrine falcon	*Falco peregrinus*	Falconiformes	26	Paired solitary or spaced cavity aggregates	Often paired	ST: KY, ME, MI, MS, NC, NJ, NY, RI, SD, WI (E); CT, NH, TX, VA (T)
Red-shouldered hawk	*Buteo lineatus*	Accipitriformes	5	Paired solitary	Solitary or in pairs	ST: IA, NJ (E); MI, WI (T)
Ross's goose	*Anser rossii*	Anseriformes	215	Colonial	Large flocks, mixed	-
Royal tern	*Thalasseus maximus*	Charadriiformes	5	Dense colonies	Compact large flocks year-round	ST: MD (E)
Sandhill crane	*Antigone canadensis*	Gruiformes	5	Paired solitary	Large flocks	ESA (E)[3]; ST: WA (E); CA (T)

Common name	Species	Order	*N*	Nesting behavior[1]	Non-breeding behavior[1]	Threat level/listing
Snow goose	*Anser caerulescens*	Anseriformes	5581	Colonial	Gregarious, flocking	-
Snowy owl	*Bubo scandiacus*	Strigiformes	21	Paired solitary	Solitary	BCC (C)[2]
Trumpeter swan	*Cygnus buccinator*	Anseriformes	28	Paired or families	Paired birds and family groups	ST: IN (E); MI, OH (T)
Willet	*Tringa semipalmata*	Charadriiformes	2	Paired solitary	Small groups	BCC (C)[2]

FUTURE OF HPAIV IN NORTH AMERICA

Under previous HPAIV dynamics seen across other regions, we would expect an increase in transmission and mortality in North America with the return of migratory birds in the fall of 2022 (Verhagen et al. 2021). Yet, some level of immunity to the circulating HPAIVs is expected given the high number of detections that occurred from winter 2021 to summer 2022. The length of immunity and degree of cross-immunity for reassorted strains is unknown; however, clade 2.3.4.4 H5 in Europe has demonstrated increased reassortment activity and outbreak events as compared to previous clades (European Food Safety Authority et al. 2022a). Along with immunity levels, the actual magnitude of disease expected with the 2022 fall migration is also unknown. If there is another increase in transmission and mortality events, it could be disastrous for sensitive colony nesting bird populations which have been disproportionately affected and includes populations and species of heightened conservation concern.

HPAIV IMPACTS ON MAMMALS AND ONE HEALTH DISEASE

The effects of HPAIV are not limited to birds; marine mammal and sporadic terrestrial mammal H5N1 infections have been detected in North America in 2022. For example, there was a MME of infected harbor and gray seals across the state of Maine Coast (n = 157) (Puryear et al. 2022) and numerous seal detections in the Gulf of St. Lawrence (n = 18). A bottlenose dolphin (*Tursiops truncatus*) infection was detected in the state of Florida. Additionally, mammal infections have included black bears (*Ursus americanus*; Canadian province: Quebec = 2), red foxes (*Vulpes vulpes*; US states: Alaska = 1; North Dakota = 3; Canadian provinces: Alberta = 6; British Columbia = 3; Manitoba = 6, Nova Scotia = 2; Ontario = 12; Prince Edward = 6; Quebec = 1; Saskatchewan = 3; Yukon = 1), striped skunks (*Mephitis mephitis*, Canadian provinces: Alberta = 14; British Columbia = 1; Manitoba = 1; Saskatchewan = 5), a fisher (*Pekania pennant*; US state: Wisconsin = 1), a beaver (*Castor canadensis*; US state: California = 1), and a mink (*Neovison vison*; Canadian province: Ontario = 1) have had infections detected after mortality ("WHISPers" 2022). This is likely indicative of food web and environmental transmission processes occurring, such as carnivorous mammals becoming infected after ingesting infected birds (Reperant et al. 2008; Rijks et al. 2021) and marine mammals becoming infected by ingestion or environmental transmission. As of November of 2022, it appears that mammalian infections have not resulted in circulating infections. However, Puryear et al. (2022) recovered a genetic mutation associated with mammalian adaptation, which indicates the potential for host adaptation and additional One Health implications. Two human infections have so far been detected: one case in January of 2022 in the United Kingdom by someone who raised residential ducks (Oliver et al. 2022); one case in April of 2022 in Colorado, USA by a person associated with infected poultry culling (CDC Newsroom 2022).

DECISION ANALYSIS FRAMEWORK TO AID EMERGENT DISEASE RESPONSE

HPAIV has created many unique issues and needs across various contexts. The high uncertainty of future North American HPAIV disease dynamics coupled with the diversity of species impacted and differences in migratory distance, behavior, and ecological context (e.g., habitat types, population size, conservation priority) create extensive biological uncertainty around any proactive disease management decisions. Challenges to decisions include the complex North American governance structures with conflicting or overlapping authorities. Additionally, resource and capacity limitations require determination of how to best allocate resources as well as inform the prioritization of urgent science and populations of highest risk for future HPAIV impacts. The likelihood of improved management and identification of urgent scientific priorities may be improved through implementation of decision analysis.

In other complex environmental issues, with competing objectives, uncertain dynamics, many stakeholders, and a complex array of management options, decision analysis processes such as structured decision making are often cited as an effective model-based decision support tool for managers (Conroy & Peterson 2013; Runge et al. 2020). Decision analysis methods have been implemented in determining mitigation and proactive management decisions for wildlife diseases including *Bsal* (*Batrachochytrium salamandrivorans*) and *Bd* (*Batrachochytrium dendrobatidis*) in amphibians (Canessa et al. 2018; Gerber et al. 2018; Bozzuto et al. 2020), and One Health diseases such as SARS-CoV-2 transmission from humans to bats (Cook et al. 2022). Decision analysis can also be implemented to determine prioritization of biological uncertainties in order to improve management outcomes (Nicol et al. 2019) and to guide management decisions in urgent and emergent disease outbreaks (Probert et al. 2018). A One Health focused decision framework encompassing wildlife, poultry, and humans may provide the tools necessary to address wildlife disease management problems where resource and knowledge limitations exist within the complex governance structures of North America.

Decision analysis provides a structured framework for characterizing, decomposing, and analyzing a management decision (Hammond et al. 2015; Runge et al. 2020). The process begins with identification of the actors, managers, scientists, and relevant stakeholders, as inclusive engagement is essential to fully capture all problem facets and ultimately to have a successful process. The PrOACT acronym is often used to identify the key elements of the decision analysis: **Pr**oblem framing to identify the decision maker and their authority to act; articulation of the decision maker’s fundamental **O**bjectives; generating **A**lternatives that may meet the objectives; building models to predict the **C**onsequences and outcomes of the alternatives in terms of meeting the objectives; and examining **T**radeoffs to identify a preferred alternative, which may require optimization before a finalized decision and action steps can be taken (Fig. 3) (Hammond et al. 2015). These steps may be nonlinear in process and are often iterative as they proceed, where iteration is necessary as the understanding and needs of the disease problem are refined. This iterative process is highly likely here given the uncertainties surrounding HPAIV.

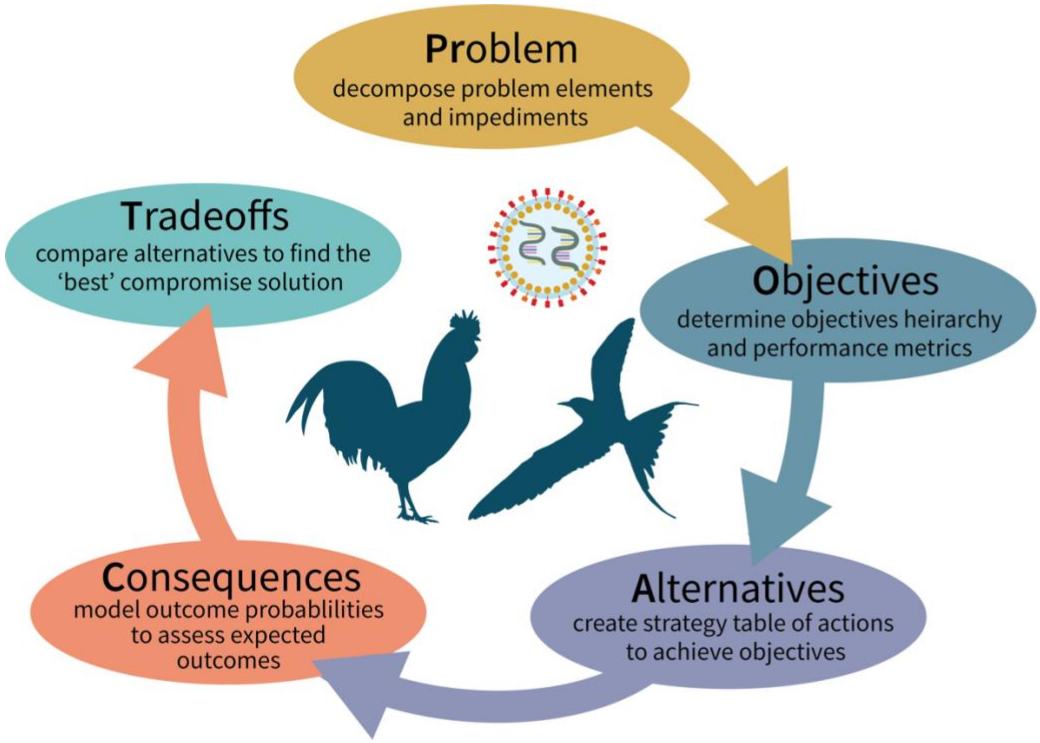
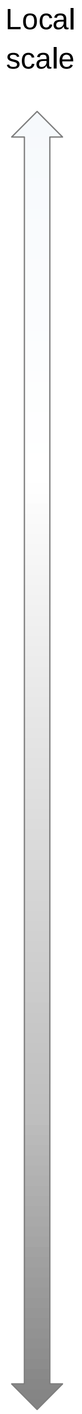


Fig. 3. Structured decision making process steps: Problem, Objective, Alternatives, Consequences and Tradeoffs, for addressing high pathogenicity avian influenza virus (HPAIV) impact on poultry and wild birds in North America. Figure adapted from (Converse et al. 2013; Runge et al. 2013).

DECISION ANALYSIS ACROSS GOVERNANCE SCALES

While decision analysis can help create a structured process for deliberation, the appropriate scale can vary from agency-level priority setting to local population management. A proper assessment of the problem and objectives needs to incorporate both science and value-based judgements and determine which scale is best equipped to address the issue. Federal and state agencies are already invested in managing bird populations. Though those agency priorities may be set at broad national and regional scales, conservation actions and implementation typically occur at local scales. Yet, addressing detections and spread of HPAIV, along with researching specific areas of uncertainty, will require decision making and coordination across various scales (e.g., county, census subdivision, regional, national agency, NA flyways, global migratory connections). Here we provide example triggers for HPAIV management problems in North America that range across governance scales and prompt the need for a management response that could benefit from a formal decision making process (Table 2). These examples include localized triggers such as detections of HPAIV in an area with a threatened colony nesting population. HPAIV as a threat for a known sensitive species should trigger a management response which may range from reservoir species deterrence or habitat manipulation to deter species use, but other options may exist and be identified through the decision making process. An example of a broad regional scale problem is determining regional or flyway prioritization of sensitive species for targeted protection. A decision focused process can further help inform the dynamics of implementation effectiveness across scales by bringing together agencies with separate authorities to improve coordination (Converse & Grant 2019).

Table 2. Examples of potential triggers and the associated decision makers and decision contexts that could benefit from a structured decision making approach, including the challenges associated, for HPAIV application in North America. Gradient arrow indicates an increase in scale from local to regional scale.



Potential Triggers	**Decision Maker**	**Problem Framing**	**Challenges**
HPAIV mortalities detected within a National Wildlife Refuge (NWR)	Refuge manager	Should carcasses be removed?	Uncertain if carcass removal mitigates AIV transmission? Uncertain if carcass handling increases human exposure?
HPAIV detection in wild birds near a poultry farm	Poultry farm manager	Can increased levels of biosecurity be enacted when disease threats are increased?	Wetlands adjacent to a farm may provide habitat for wildlife. How can that risk be mitigated?
HPAIV detected in area with a threatened colony nesting population	Landowner where the population occurs/ agency responsible for threatened species	What actions can be taken to protect sensitive species?	Do actions favorably impact all nesting species in a mixed species nesting site?
Prior loss or decline due to HPAIV in a sensitive species/population	State wildlife agency	Can future population decline due to HPAIV be prevented? Can populations be managed independently to protect species persistence?	Level of immunity and cross-immunity in species not known Lack of information on population sizes or stability for many sensitive populations/species
HPAIV impact on multi-use and public access areas (state park, National Forest, NWR)	State Park manager, National Forest superintendent, or Refuge manager	Should public use be curtailed to decrease disease spread?	Disease mitigation may undermine ability to achieve public use objectives (i.e., difficult tradeoffs need to be navigated).
HPAIV detected in wild birds or poultry during waterfowl hunting season	U.S. Fish and Wildlife Service, or state wildlife agency	What measures or restrictions within the area of detection will reduce spread? Can hunting continue safely?	Uncertainty about how hunting contributes to disease transmission and dispersal.

	Potential Triggers	Decision Maker	Problem Framing	Challenges
	HPAIV detection during fall waterfowl banding	U.S. Fish and Wildlife Service, Canadian Wildlife Service	Should banding be stopped, to prevent aggregation of birds and transmission at banding sites?	Banding is essential for long term population monitoring. Uncertain if banding impacts transmission?
	Limited capacity/funding for disease surveillance and response	Multiple agencies that need to coordinate	How can capacity and resources best be used for effective disease management/response?	Funding and capacity are multi-scale problems, and the responsive agencies might not have a governance structure that allows or promotes collaboration and sharing of resources
Regional scale	Continued HPAIV persistence in North American flyway	North American Flyway Councils	Can sensitive species be protected? Can surveillance strategies improve prioritization objectives?	Impacts on birds are geographically widespread

North America now faces a future with increased probability of recurrent HPAIV epizootics affecting wildlife, captive species, and poultry, with the potential for major economic damage and impacts on food security. Wildlife agencies, industry managers, and public health officials are beginning to feel urgency to accelerate the ability to make sound decisions in the face of uncertainty, which may be helped by using decision making processes to address species of conservation concern, sensitive management areas, and high poultry production areas. A decision analysis framework, specifically structured decision making, for response to HPAIV mitigation and management across scales could provide a model-based decision tool for other managers and decision makers and would facilitate the implementation of a more efficient, effective wildlife disease decision making processes. The process of decision analysis may identify actions which are robust to the uncertainties of the HPAIV disease system, such as actions to protect sensitive species which will benefit from improved conservation efforts.

USING DECISION ANALYSIS TO DRIVE SCIENTIFIC INQUIRY

Much of the complexity of this and other emergent disease systems is the inherent degree of epistemic uncertainty (biological or ecological) due to the dynamic nature of viral disease ecology and the vagility of migrant birds. Value of information methods can be used within a decision framework to identify the science that will most improve management and conservation actions (Shea et al. 2014). Thus, scientific inquiry can be targeted to reduce scientific uncertainties that are most relevant to decision makers. Several, but not all uncertainties for management have been identified (Table 2), such as whether carcass removal will reduce HPAI transmission or whether hunting impacts disease transmission. Additionally, whether asymptomatic infections may affect the subsequent infection seasons by resulting in increased dispersal by migratory species and thereby impacting the persistence of virus in North American birds.

CONCLUSIONS

The impacts of future North American HPAIV dynamics are of broad concern from a One Health perspective and could benefit from an inclusive decision making approach. Processes and tools to increase the effectiveness of decision making and better prioritize conservation strategies could be employed. The future of HPAIV in North America is unclear and may be impacted by continued reassortment of HPAIV H5N1 with other LPAIV commonly present in wildlife and the resultant fitness of viral lineages. North America has seen a high amount of mortality in this first infection season occurring in 2021-2022, and the degree of asymptomatic spread that has occurred and gone undetected is unclear. The changing dynamics of HPAIV along with possibility of clade 2.3.4.4b HPAIV persistence in North American through continued asymptomatic circulation or environmental persistence, is unknown. This lack of knowledge is compounded by the fact that a broad range of host species with diverse migratory and life history strategies are being impacted and management must occur across multiple scales. Given the high levels of uncertainty, SDM could be an effective framework to identify management concerns and priorities that can provide a path toward targeted science to support effective management. Decision analysis may be used to inform the prioritization of management needs and further value of information methods may be implemented to inform the research agenda for scientific inquiry.

ACKNOWLEDGMENTS

We would like to thank the following for help with the wild bird detection data: Krista Dilione at USDA/APHIS, Robert Dusek and Neil Baertlein at USGS with the WHISPers administration team, and Shannon French and Julie Paré with CFIA/ACIA for help with data from the Canadian National Influenza Database. We would like to thank Andrew Ramey (USGS) and Margaret McEachran (USGS/University of Massachusetts Amherst) for comments to strengthen the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Ahrens, A.K., Selinka, H.-C., Mettenleiter, T.C., Beer, M. & Harder, T.C. (2022). Exploring surface water as a transmission medium of avian influenza viruses – systematic infection studies in mallards. *Emerging Microbes & Infections*, 11, 1250–1261.

Alkie, T.N., Lopes, S., Hisanaga, T., Xu, W., Suderman, M., Koziuk, J., Fisher, M., Redford, T., Lung, O., Joseph, T., Himsworth, C.G., Brown, I.H., Bowes, V., Lewis, N.S. & Berhane, Y. (2022). A threat from both sides: Multiple introductions of genetically distinct H5 HPAI viruses into Canada via both East Asia-Australasia/Pacific and Atlantic flyways. *Virus Evolution*, 8, veac077.

Animal and Plant Health Inspection Service, Veterinary Services & National Preparedness and Incident Coordination. (2016). *Final Report for the 2014–2015 Outbreak of Highly Pathogenic Avian Influenza (HPAI) in the United States*. USDA.

Ann, V. (2022). Strain of highly pathogenic avian influenza kills thousands of birds in Quebec [WWW Document]. *CBC News*. URL https://www.cbc.ca/news/canada/montreal/strain-highly-pathogenic-avian-influenza-quebec-1.6474289 (accessed 08.30.2022).

Antigua, K.J.C., Choi, W.-S., Baek, Y.H. & Song, M.-S. (2019). The Emergence and Decennary Distribution of Clade 2.3.4.4 HPAI H5Nx. *Microorganisms*, 7, 156.

Becker, W.B. (1966). The isolation and classification of Tern virus: Influenza Virus A/Tern/South Africa/1961. *Epidemiology & Infection*, 64, 309–320.

Bevins, S.N., Dusek, R.J., White, C.L., Gidlewski, T., Bodenstein, B., Mansfield, K.G., DeBruyn, P., Kraege, D., Rowan, E., Gillin, C., Thomas, B., Chandler, S., Baroch, J., Schmit, B., Grady, M.J., Miller, R.S., Drew, M.L., Stopak, S., Zscheile, B., Bennett, J., Sengl, J., Brady, C., Ip, H.S., Spackman, E., Killian, M.L., Torchetti, M.K., Sleeman, J.M. & Deliberto, T.J. (2016). Widespread detection of highly pathogenic H5 influenza viruses in wild birds from the Pacific Flyway of the United States. *Sci Rep*, 6, 28980.

Bevins, S.N., Shriner, S.A., Jr, J.C.C., Dilione, K.E., Douglass, K.E., Ellis, J.W., Killian, M.L., Torchetti, M.K. & Lenoch, J.B. (2022). Intercontinental Movement of Highly Pathogenic Avian Influenza A(H5N1) Clade 2.3.4.4 Virus to the United States, 2021. *Emerging Infectious Diseases*, 28, 6.

Lester, G.Bird flu has killed nearly 1,500 threatened Caspian terns on Lake Michigan islands. (2022). *Michigan Radio*. URL https://www.michiganradio.org/environment-climate-change/2022-06-29/bird-flu-has-killed-nearly-1-500-threatened-caspian-terns-on-lake-michigan-islands. (accessed 08.27.2022).

Bozzuto, C., Schmidt, B.R. & Canessa, S. (2020). Active responses to outbreaks of infectious wildlife diseases: objectives, strategies and constraints determine feasibility and success. *Proc. R. Soc. B.*, 287, 20202475.

Caliendo, V., Lewis, N.S., Pohlmann, A., Baillie, S.R., Banyard, A.C., Beer, M., Brown, I.H., Fouchier, R.A.M., Hansen, R.D.E., Lameris, T.K., Lang, A.S., Laurendeau, S., Lung, O., Robertson, G., van der Jeugd, H., Alkie, T.N., Thorup, K., van Toor, M.L., Waldenström, J., Yason, C., Kuiken, T. & Berhane, Y. (2022). Transatlantic spread of highly pathogenic avian influenza H5N1 by wild birds from Europe to North America in 2021. *Sci Rep*, 12, 11729.

Canadian Food Inspection Agency Government of Canada. (2022). Status of ongoing avian influenza response by province. URL https://inspection.canada.ca/animal-health/terrestrial-animals/diseases/reportable/avian-influenza/hpai-in-canada/status-of-ongoing-avian-influenza-response/eng/1640207916497/1640207916934. (accessed 11.13.2022)

Canessa, S., Bozzuto, C., Campbell Grant, E.H., Cruickshank, S.S., Fisher, M.C., Koella, J.C., Lötters, S., Martel, A., Pasmans, F., Scheele, B.C., Spitzen-van der Sluijs, A., Steinfartz, S. & Schmidt, B.R. (2018). Decision-making for mitigating wildlife diseases: From theory to practice for an emerging fungal pathogen of amphibians. *Journal of Applied Ecology*, 55, 1987–1996.

CDC Newsroom. (2022). *U.S. Case of Human Avian Influenza A(H5) Virus Reported*. CDC. (accessed 10.12.2022)

Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.S.A.*, 114.

Chapter 10.4 Infection with high pathogenicity avian influenza viruses. (2021). In: *OIE Terrestrial Animal Health Code*. World Organization for Animal Health.

Chardine, J.W., Rail, J.-F. & Wilhelm, S. (2013). Population dynamics of Northern Gannets in North America, 1984-2009: Northern Gannet Population Dynamics. *Journal of Field Ornithology*, 84, 187–192.

Claus O. Wilke. (2022). ggridges: Ridgeline Plots in “ggplot2.”

CMS & FAO. (2022). *Scientific Task Force on Avian Influenza and Wild Birds statement. H5N1 Highly Pathogenic Avian Influenza in poultry and wild birds: Winter of 2021/2022 with focus on mass mortality of wild birds in UK and Israel*. Scientific Task Force on Avian Influenza and Wild Birds.

Conroy, M.J. & Peterson, J.T. (2013). *Decision making in natural resource management: a structured, adaptive approach*. Wiley, Hoboken, NJ.

Converse, S.J. & Grant, E.H.C. (2019). A three-pipe problem: dealing with complexity to halt amphibian declines. *Biological Conservation*, 236, 107–114.

Converse, S.J., Moore, C.T. & Armstrong, D.P. (2013). Demographics of reintroduced populations: Estimation, modeling, and decision analysis: Demographics of Reintroduced Populations. *Jour. Wild. Mgmt.*, 77, 1081–1093.

Cook, J.D., Campbell Grant, E.H., Coleman, J.T.H., Sleeman, J.M. & Runge, M.C. (2022). Evaluating the risk of SARS-CoV-2 transmission to bats in the context of wildlife research, rehabilitation, and control. *Wildlife Society Bulletin*, 46.

Cui, P., Shi, J., Wang, C., Zhang, Y., Xing, X., Kong, H., Yan, C., Zeng, X., Liu, L., Tian, G., Li, C., Deng, G. & Chen, H. (2022). Global dissemination of H5N1 influenza viruses bearing the clade 2.3.4.4b HA gene and biologic analysis of the ones detected in China. *Emerging Microbes & Infections*, 11, 1693–1704.

EMPRES. (2022). *Disease reports of avian inluenza H5N1 from January 2014 - November 2022*. FAO United Nations. (accessed 11.25,2022).

European Food Safety Authority, European Centre for Disease Prevention and Control, European Union Reference Laboratory for Avian Influenza, Adlhoch, C., Fusaro, A., Gonzales, J.L., Kiuiken, T., Marangon, S., Niquex, É., Staubach, C., Terregino, C., Aznar, I., Muñoz Guajardo, I. & Baldineli, F. (2022a). Avian influenza overview December 2021 – March 2022. *EFS2*, 20, 7289.

European Food Safety Authority, European Centre for Disease Prevention and Control, European Union Reference Laboratory for Avian Influenza, Adlhoch, C., Fusaro, A., Gonzales, J.L., Kuiken, T., Marangon, S., Niqueux, É., Staubach, C., Terregino, C., Aznar, I., Guajardo, I.M. & Baldinelli, F. (2022b). Avian influenza overview March – June 2022. *EFS2*, 20.

Fouchier, R. & Munster, V. (2009). Epidemiology of low pathogenic avian influenza viruses in wild birds: -EN- Epidemiology of low pathogenic avian influenza viruses in wild birds -FR- Epidemiologie des virus de l'influenza aviaire faiblement pathogène dans l'avifaune -ES- Epidemiología de la influenza aviar de baja patogenicidad en aves silvestres. *Rev. Sci. Tech. OIE*, 28, 49–58.

Gerber, B.D., Converse, S.J., Muths, E., Crockett, H.J., Mosher, B.A. & Bailey, L.L. (2018). Identifying Species Conservation Strategies to Reduce Disease-Associated Declines: Optimal conservation strategy. *Conservation Letters*, 11, e12393.

Hammond, J.S., Keeney, R.L. & Raiffa, H. (2015). *Smart Choices: a practical guide to making better decisions*. Harvard Business School : McGraw-Hill, Boston, Mass., London.

Hill, N.J., Bishop, M.A., Trovão, N.S., Ineson, K.M., Schaefer, A.L., Puryear, W.B., Zhou, K., Foss, A.D., Clark, D.E., MacKenzie, K.G., Gass, J.D., Borkenhagen, L.K., Hall, J.S. & Runstadler, J.A. (2022). Ecological divergence of wild birds drives avian influenza spillover and global spread. *PLoS Pathog*, 18, e1010062.

Ip, H.S., Torchetti, M.K., Crespo, R., Kohrs, P., DeBruyn, P., Mansfield, K.G., Baszler, T., Badcoe, L., Bodenstein, B., Shearn-Bochsler, V., Killian, M.L., Pedersen, J.C., Hines, N., Gidlewski, T., DeLiberto, T. & Sleeman, J.M. (2015). Novel Eurasian Highly Pathogenic Avian Influenza A H5 Viruses in Wild Birds, Washington, USA, 2014. *Emerg Infect Dis*, 21, 886–890.

Kang, H.-M., Lee, E.-K., Song, B.-M., Jeong, J., Choi, J.-G., Jeong, J., Moon, O.-K., Yoon, H., Cho, Y., Kang, Y.-M., Lee, H.-S. & Lee, Y.-J. (2015). Novel Reassortant Influenza A(H5N8) Viruses among Inoculated Domestic and Wild Ducks, South Korea, 2014. *Emerg. Infect. Dis.*, 21, 298–304.

Lee, D.-H., Bertran, K., Kwon, J.-H. & Swayne, D.E. (2017). Evolution, global spread, and pathogenicity of highly pathogenic avian influenza H5Nx clade 2.3.4.4. *J Vet Sci*, 18, 269.

Lee, D.-H., Torchetti, M.K., Winker, K., Ip, H.S., Song, C.-S. & Swayne, D.E. (2015). Intercontinental Spread of Asian-Origin H5N8 to North America through Beringia by Migratory Birds. *J Virol*, 89, 6521–6524.

Li, Y., Li, M., Li, Y., Tian, J., Bai, X., Yang, C., Shi, J., Ai, R., Chen, W., Zhang, W., Li, J., Kong, Y., Guan, Y. & Chen, H. (2020). Outbreaks of Highly Pathogenic Avian Influenza (H5N6)

Virus Subclade 2.3.4.4h in Swans, Xinjiang, Western China, 2020. *Emerg. Infect. Dis.*, 26, 2956–2960.

National Avian Influenza - Wild Positives [WWW Document]. (2022). . URL https://cfia-ncr.maps.arcgis.com/apps/dashboards/89c779e98cdf492c899df23e1c38fdbc. (accessed 10.07.2022).

Neumann, G., Chen, H., Gao, G.F., Shu, Y. & Kawaoka, Y. (2010). H5N1 influenza viruses: outbreaks and biological properties. *Cell Res*, 20, 51–61.

Nicol, S., Brazill-Boast, J., Gorrod, E., McSorley, A., Peyrard, N. & Chadès, I. (2019). Quantifying the impact of uncertainty on threat management for biodiversity. *Nat Commun*, 10, 3570.

Oliver, I., Roberts, J., Brown, C.S., Byrne, A.M., Mellon, D., Hansen, R.D., Banyard, A.C., James, J., Donati, M., Porter, R., Ellis, J., Cogdale, J., Lackenby, A., Chand, M., Dabrera, G., Brown, I.H. & Zambon, M. (2022). A case of avian influenza A(H5N1) in England, January 2022. *Eurosurveillance*, 27.

Olsen, B., Munster, V.J., Wallensten, A., Waldenström, J., Osterhaus, A.D.M.E. & Fouchier, R.A.M. (2006). Global Patterns of Influenza A Virus in Wild Birds. *Science*, 312, 384–388.

Pohlmann, A., King, J., Fusaro, A., Zecchin, B., Banyard, A.C., Brown, I.H., Byrne, A.M.P., Beerens, N., Liang, Y., Heutink, R., Harders, F., James, J., Reid, S.M., Hansen, R.D.E., Lewis, N.S., Hjulsager, C., Larsen, L.E., Zohari, S., Anderson, K., Bröjer, C., Nagy, A., Savič, V., van Borm, S., Steensels, M., Briand, F.-X., Swieton, E., Smietanka, K., Grund, C., Beer, M. & Harder, T. (2022). Has Epizootic Become Enzootic? Evidence for a Fundamental Change in the Infection Dynamics of Highly Pathogenic Avian Influenza in Europe, 2021. *mBio*, e00609-22.

Probert, W.J.M., Jewell, C.P., Werkman, M., Fonnesbeck, C.J., Goto, Y., Runge, M.C., Sekiguchi, S., Shea, K., Keeling, M.J., Ferrari, M.J. & Tildesley, M.J. (2018). Real-time decision-making during emergency disease outbreaks. *PLoS Comput Biol*, 14, e1006202.

Puryear, W., Sawatzki, K., Hill, N., Foss, A., Stone, J.J., Doughty, L., Walk, D., Gilbert, K., Murray, M., Cox, E., Patel, P., Mertz, Z., Ellis, S., Taylor, J., Fauquier, D., Smith, A., DiGiovanni, R.A., van de Guchte, A., Gonzalez-Reiche, A.S., Khalil, Z., van Bakel, H., Torchetti, M.K., Lenoch, J.B., Lantz, K. & Runstadler, J. (2022). Outbreak of Highly Pathogenic Avian Influenza H5N1 in New England Seals.

Ramey, A.M., Hill, N.J., DeLiberto, T.J., Gibbs, S.E.J., Camille Hopkins, M., Lang, A.S., Poulson, R.L., Prosser, D.J., Sleeman, J.M., Stallknecht, D.E. & Wan, X.F. (2022). Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America. *Journal of Wildlife Management*, 86, 1–21.

Ramey, A.M., Reeves, A.B., Drexler, J.Z., Ackerman, J.T., De La Cruz, S., Lang, A.S., Leyson, C., Link, P., Prosser, D.J., Robertson, G.J., Wight, J., Youk, S., Spackman, E., Pantin-Jackwood, M., Poulson, R.L. & Stallknecht, D.E. (2020). Influenza A viruses remain infectious for more than seven months in northern wetlands of North America: IAVs in wetlands. *Proceedings of the Royal Society B: Biological Sciences*, 287.

Ramey, A.M., Reeves, A.B., TeSlaa, J.L., Nashold, S., Donnelly, T., Bahl, J. & Hall, J.S. (2016). Evidence for common ancestry among viruses isolated from wild birds in beringia and highly pathogenic intercontinental reassortant H5N1 and H5N2 influenza a viruses. *Infection, Genetics and Evolution*, 40, 176–185.

Ramos, S., MacLachlan, M. & Melton, A. (2017). *Impacts of the 2014-2015 Highly Pathogenic Avian Influenza Outbreak on the U.S. Poultry Sector* (No. LPDM-282-02).

Reperant, L.A., van Amerongen, G., van de Bildt, M.W.G., Rimmelzwaan, G.F., Dobson, A.P., Osterhaus, A.D.M.E. & Kuiken, T. (2008). Highly Pathogenic Avian Influenza Virus (H5N1) Infection in Red Foxes Fed Infected Bird Carcasses. *Emerg. Infect. Dis.*, 14, 1835–1841.

Rijks, J.M., Hesselink, H., Lollinga, P., Wesselman, R., Prins, P., Weesendorp, E., Engelsma, M., Heutink, R., Harders, F., Kik, M., Rozendaal, H. & Beerens, N. (2021). Highly Pathogenic Avian Influenza A(H5N1) Virus in Wild Red Foxes, the Netherlands, 2021. *Emerging Infectious Diseases*, 27, 2960–2962.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M. & Marra, P.P. (2019). Decline of the North American avifauna. *Science*, 366, 120–124.

Rowan, M.K. (1962). Mass mortality among European Common Terns in South Africa in April-May 196. *British Birds*, 55, 103–114.

Runge, M.C., Grand, J.B. & Mitchell, M.S. (2013). Structured Decision Making. In: *Wildlife Management and Conservation: Contemporary Principles and Practices*. Johns Hopkins University Press, Baltimore, MD, pp. 51–72.

Runge, M.C., Sarah J. Converse, James E. Lyons, & David R. Smith (eds.). (2020). *Structured decision making: case studies in natural resource management*. Wildlife management and conservation. Johns Hopkins University Press, Baltimore.

Sauer, J.R., Link, W.A. & Hines, J.E. (2020). *The North American Breeding Bird Survey, Analysis Results 1966 - 2019*. U.S. Geological Survey data release.

Shea, K., Tildesley, M.J., Runge, M.C., Fonnesbeck, C.J. & Ferrari, M.J. (2014). Adaptive Management and the Value of Information: Learning Via Intervention in Epidemiology. *PLOS Biology*, 12, e1001970.

Suarez, D.L. (2008). Influenza A Virus. In: *Avian influenza* (ed. Swayne, D.E.). Blackwell Pub, Ames, Iowa.

Swayne, D.E. & Suarez, D.L. (2000). Highly pathogenic avian influenza. *Revue of Science and Technology of the Office International des Epizooties*, 19, 463–482.

USDA APHIS. (2022a). 2022 Detections of Highly Pathogenic Avian Influenza in Wild Birds. URL https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/animal-disease-information/avian/avian-influenza/hpai-2022/2022-hpai-wild-birds. (accessed 10.25.2022)

USDA APHIS. (2022b). 2022 Confirmations of Highly Pathogenic Avian Influenza in Commercial and Backyard Flocks [WWW Document]. URL https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/animal-disease-information/avian/avian-influenza/hpai-2022/2022-hpai-commercial-backyard-flocks. (accessed 11.13.2022)

Verhagen, J.H., Fouchier, R.A.M. & Lewis, N. (2021). Highly Pathogenic Avian Influenza Viruses at the Wild–Domestic Bird Interface in Europe: Future Directions for Research and Surveillance. *Viruses*, 13, 212.

de Vries, E., Guo, H., Dai, M., Rottier, P.J.M., van Kuppeveld, F.J.M. & de Haan, C.A.M. (2015). Rapid Emergence of Highly Pathogenic Avian Influenza Subtypes from a Subtype H5N1 Hemagglutinin Variant. *Emerg. Infect. Dis.*, 21, 842–846.

Webster, R.G., Bean, W.J., Gorman, O.T., Chambers, T.M. & Kawaoka, Y. (1992). Evolution and ecology of influenza A viruses. *MICROBIOL. REV.*, 56, 28.

WHISPers. (2022). URL https://whispers.usgs.gov/home. (accessed 10.26.2022).

WHO/OIE/FAO H5N1 Evolution Working Group. (2008). Toward a Unified Nomenclature System for Highly Pathogenic Avian Influenza Virus (H5N1). *Emerg. Infect. Dis.*, 14, e1–e1.

World Health Organization. (2022). *Antigenic and genetic characteristics of zoonotic influenza A viruses and development of candidate vaccine viruses for pandemic preparedness*. World Health Organization.

Xu, X., Subbarao, K., Cox, N.J. & Guo, Y. (1999). Genetic Characterization of the Pathogenic Influenza A/Goose/Guangdong/1/96 (H5N1) Virus: Similarity of Its Hemagglutinin Gene to Those of H5N1 Viruses from the 1997 Outbreaks in Hong Kong. *Virology*, 261, 15–19.