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Weathering the Storm of High Pathogenicity Avian Influenza in Waterbirds

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Abstract.—The ongoing panzootic of bird flu caused by high pathogenicity avian influenza (HPAI) virus is unprecedented in scale, with mass mortality events causing population level effects for several waterbird species. While the panzootic commenced in 2021, a number of key events have occurred over the past decades leading to the emergence of this viral lineage. Since 2021, tens of thousands of outbreaks have occurred affecting at least 320 species belonging to 21 orders, of which the vast majority are waterbirds. In this report we provide examples from across the globe associated with population level declines. Only Australia and Antarctica are unaffected, although this could change rapidly. Despite the carnage caused by mass mortality events, there are strategies to better protect waterbirds in both the short and long term. These include prevention of further spillover events from poultry, designing improved surveillance systems to both inform virus epidemiology and to benefit of all wild birds rather than only poultry (and humans), and respond appropriately to outbreaks in wildlife with necessary detail and resources. The loss of waterbirds at the current scale will not only be a conservation disaster, but also an ecological disaster, and therefore response to outbreaks in waterbirds must be prioritized.

Key words.—avian influenza, opinion

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What is Bird Flu?

Infectious agents are ubiquitous, and like most animals, waterbirds (avian taxa that rely on freshwater or marine ecosystems) are host to a large diversity of parasites and microbes. However, what we see with the current “bird flu” panzootic is unprecedented in magnitude and impact on waterbirds across the globe. So, what is bird flu? Waterbirds are well known reservoirs for low pathogenicity avian influenza (LPAI) viruses, with infections that do not cause observable clinical disease in the natural host reservoir: Anseriformes (ducks, geese, and swans) and Charadriiformes (shorebirds, gulls, alcids) (Olson *et al.* 2006). LPAI have co-evolved and diversified within waterbird hosts, with 16 hemagglutinin (HA) and 9 neuraminidase (NA) subtypes found in waterbirds. Surveillance of *Anas* duck populations in the temperate Northern Hemisphere has demonstrated that LPAI viruses are very common. For example, between 10–20% of Mallards (*Anas platyrhynchos*) may be infected on any

given day during the autumn (Latorre-Margalef *et al.* 2014), and it is likely that the vast majority of individuals have had at least one infection by winter.

This is in contrast to high pathogenicity avian influenza (HPAI) virus, often referred to as “bird flu.” HPAI viruses emerge from H5 or H7 subtype LPAI viruses in poultry, and the emergent HPAI viruses are much more virulent and cause systemic disease in contrast to LPAI viruses that predominantly infect the lower gastrointestinal tract (Monne *et al.* 2014). HPAI viruses have not (yet) co-evolved with wild birds and are not a natural part of the virome, and therefore cause substantial mortality when they spill over from poultry into wild waterbirds. The current panzootic is caused by one of these HPAI viruses, referred to as clade 2.3.4.4b HPAI H5N1, designating the specific viral clade and subtype (Fig 1).

A Brief History of HPAI H5

Despite current global attention, HPAI is not a new problem. The earliest reports

What does “clade 2.3.4.4b HPAI H5N1” mean?

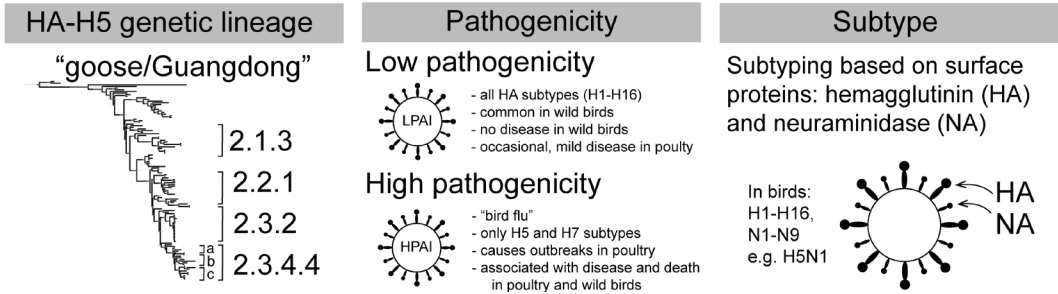


Figure 1. Avian influenza classification schemes, designating viral clade, pathogenicity and subtype.

extend back to the late 1800’s (Worobey *et al.* 2014) and historically outbreaks occurred very infrequently. The situation changed with the emergence of the goose/Guangdong (Gs/Gd) HPAI H5 clade. While HPAI viruses are typically eradicated with stamping out efforts in poultry, the Gs/Gd clade has been enduring (Lycett *et al.* 2019; Wille and Barr 2022), and the virus causing the current panzootic, 2.3.4.4b HPAI H5N1, is a genetic subgroup of the Gs/Gd clade.

A number of key events have occurred in the history of Gs/Gd viruses (Lycett *et al.* 2019). The first detection of Gs/Gd HPAI H5N1 was in commercial geese in Asia in 1996 (Xu *et al.* 1999) and was believed to originate from precursor LPAI H5 viruses in migratory waterbirds (Duan *et al.* 2008). Between 1997 and 2003, Gs/Gd-like strains became widespread in poultry (Chan 2002; Guan *et al.* 2002; Shortridge *et al.* 1998). With time, this virus evolved, resulting in many different clades.

In 2005, a substantial mortality event in waterbirds occurred in Qinghai Lake in west China (Chen *et al.* 2005), after which the virus rapidly spread to other parts of Asia, Europe and Africa (Salzberg *et al.* 2007). In 2014, there was a shift in epidemiology with the emergence of a new clade, referred to as clade 2.3.4.4 which replaced many of the older established clades (Global Consortium for H5N8 and Related Influenza Viruses 2016). Associated with 2.3.4.4 was long distance dispersal of the virus with outbound migratory wa-

terfowl, to both Europe and North America (Verhagen *et al.* 2015). While this virus went extinct in North America (Krauss *et al.* 2016), there were recurring outbreaks in Europe associated with the arrival of migratory waterbirds from their Siberian breeding areas (Verhagen *et al.* 2015; Zhang *et al.* 2023). The virus remained entrenched in poultry populations in Asia, and prior to 2016, waterbirds were repeatedly infected by poultry rather than acting as long-term reservoirs for this virus. However, as of 2016, there has been evidence of maintained circulation of 2.3.4.4 H5Nx viruses in European waterbirds (Poen *et al.* 2018).

HPAI activity increased in 2020 and the current, ongoing HPAI panzootic commenced in 2021 following a genetic change in the virus. Specifically, this panzootic coincided with the replacement of all circulating clades with an 2.3.4.4b clade HPAI H5 in combination with the N1 neuraminidase subtype. As a result, the number of outbreaks in wild birds (particularly waterbirds) and poultry exploded (European Food Safety Authority *et al.* 2023). In November 2021, HPAI H5 again entered North America, through both an introduction across the Atlantic Ocean via Newfoundland (Caliendo *et al.* 2022), and the Pacific Ocean (Alkie *et al.* 2022). Starting in ~October 2022, HPAI entered South America for the first time (Gamarrá-Toledo *et al.* 2023). Data currently suggests at least 3 introductions to the continent (Ruiz-Sanez *et al.* 2023). Australia and Antarctica are the only continents still free

of HPAI (as of July 2023; Wille and Klaassen 2023); however, the virus has been recorded in Tierra del Fuego and Indonesia (European Food Safety Authority *et al.* 2023), resulting in a fine barrier between affected regions and the final unaffected continents.

The current panzootic deviates dramatically from previous outbreak waves due to the global scale, the length of time of high activity, the entrenchment of the virus in wild bird populations and the diversity of wild birds affected. First, the global scale is substantially larger than any previous outbreak waves, including 2005, 2014, and 2016 (Xie *et al.* 2022). This is due to a combination of long-distance viral movements, multiple incursion events into “new” continents, and rapid speed of viral movement. For example, while there has been repeated viral spread from Asia to Europe (e.g. 2005, 2014, 2016), Africa (e.g., 2016), and North America (2014; Fusaro *et al.* 2019; Global Consortium for H5N8 and Related Influenza Viruses 2016; Keawcharoen *et al.* 2008; Verhagen *et al.* 2015) 2.3.4.4b HPAI H5N1 has spread to all continents within 2 years (Ariyama *et al.* 2023, Caliendo *et al.* 2022; Gamarra-Toledo *et al.* 2023; Harvey *et al.* 2023; Klaassen and Wille 2023). Further, following introduction to South America, this virus spread a staggering 6000 km along the length of South America in < 6 months. While previous waves have been discrete, with distinct periods of high activity (winter) and low or no activity (summer), and with multiple examples of the virus going extinct in wild waterbirds (e.g., 2005, 2014), this panzootic is characterized by constant high-level activity in wild birds, with outbreaks occurring throughout the year (European Food Safety Authority *et al.* 2023). These changes have likely occurred due to entrenchment of HPAI in wild waterbird populations, driven by efficient replication in waterbirds (particularly ducks; Foret-Lucas *et al.* 2023; James *et al.* 2023). In prior outbreaks, HPAI was still a preferentially poultry-adapted virus and therefore outbreaks in wild waterbirds were routinely seeded from poultry, which explains extinction of HPAI from Europe in 2005, and North American in 2014 (e.g.,

Krauss *et al.* 2016). Finally, with this panzootic, there has been a staggering expansion in the host range. To date, 320 species belonging to 21 orders has been affected, the vast majority of which are waterbirds (e.g., orders Anseriformes, Charadriiformes, Pelecaniformes, Podicipediformes, Suliformes; Klaassen and Wille 2023), comprising tens of thousands of outbreak notifications. Beyond wild birds, there have been numerous cases of HPAI in mammals (European Food Safety Authority *et al.* 2023), most of which were likely infected through the consumption of infected birds. While mammalian cases have been implicated in previous outbreaks (including 2005; Thiry *et al.* 2007), the geographic scale and number of mammalian species, including marine mammals, is unprecedented.

Waterbird Populations are Negatively Impacted by the Current HPAI Panzootic

A key feature of this panzootic is the scale, both in number but also magnitude, of mass mortality events in wild waterbirds (Fig. 2). One of the first reported outbreaks occurred in wintering Barnacle Geese (*Branta leucopsis*) in Scotland, where approximately one third of the Svalbard breeding population died (13,200 individuals (Promed Mail 2021; RSPB 2023; Wille and Barr 2022). An additional 5000 Greenland breeding Barnacle Geese died in Scotland in the following winter, comprising ~10% of the Greenland population. The death of 5,200 Common Cranes (*Grus grus*) in Israel (Promed Mail 2021; Wille and Barr 2022) were also recorded at the end of 2021. Commencing in 2022, a series of outbreaks decimated colony nesting birds in Europe. Approximately 2286 Dalmatian Pelicans (*Pelecanus crispus*) died in March 2022 in Greece (Alexandrou *et al.* 2022) such that > 40% of the south-east European population was lost. During the 2022 breeding season, > 20,000 Sandwich Terns (*Thalasseus sandwicensis*) were found dead across Europe, comprising > 17% of the total northwestern European breeding population. In addition to the adult birds, within colonies, almost all chicks died (Knief *et al.*

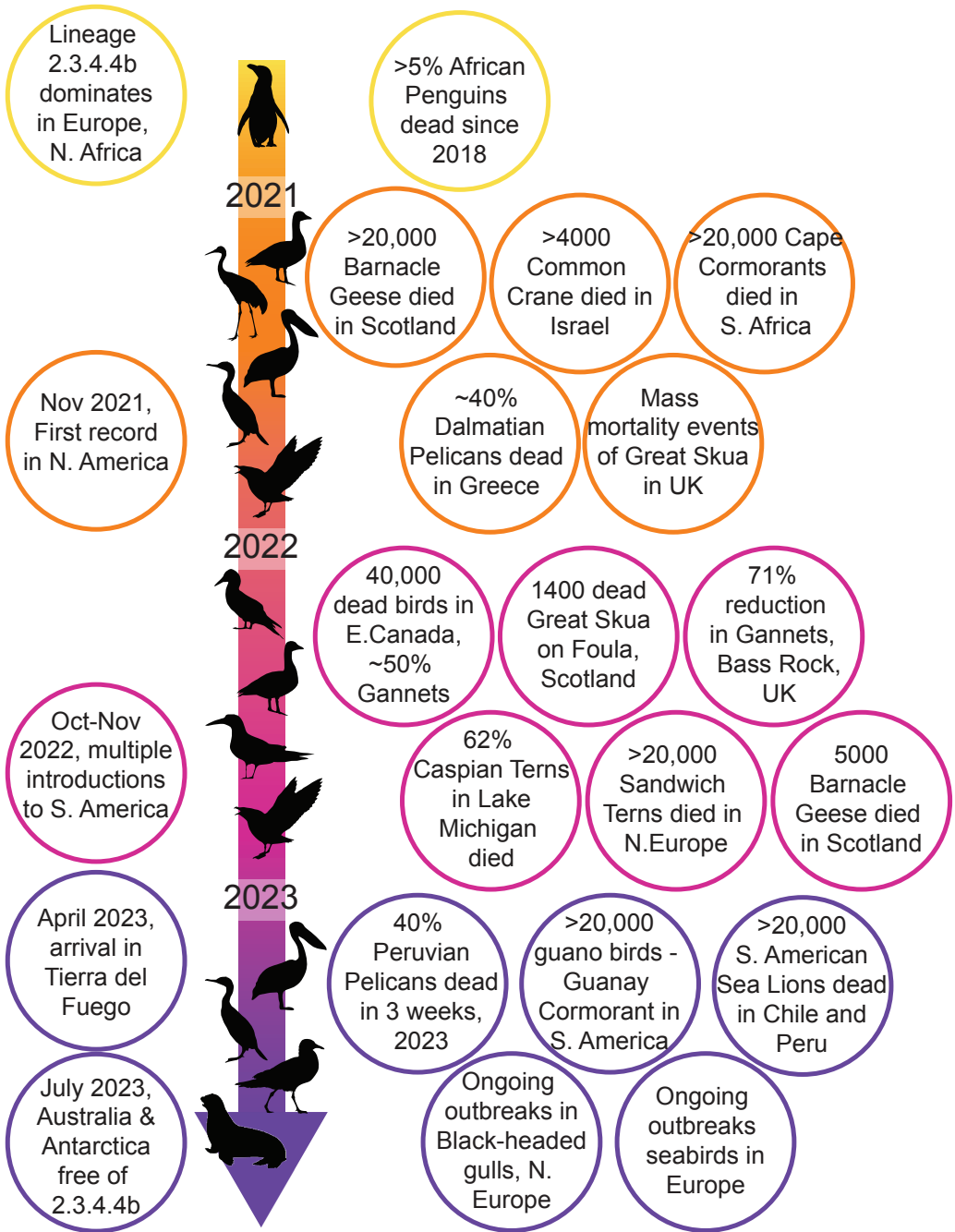


Figure 2. Notable mass mortality events in waterbirds due to 2.3.4.4b since the start of the panzootic. Outbreaks are coloured by year of occurrence (prior to 2021 yellow, 2021 orange, 2022 pink, 2023 purple). Outbreaks within each year are not presented in order. Silhouettes from phylopic.com and distributed under creative commons attributions.

2023). Northern Gannets (*Morus bassanus*) were similarly heavily affected in the Atlantic, with unusually high mortality at colonies,

including at Bass Rock in Scotland where the number of occupied nests decreased by 71% (Lane *et al.* 2023). The total number of dead

gannets is unknown, but in Canada tens of thousands likely died (pers. comm. Avery Gomm; CBC 2023). In North America, 62% of Caspian Terns (*Hydroprogne caspia*) breeding on Lake Michigan died in 2022 (Harvey *et al.* 2023).

By 2023, substantial outbreaks began occurring in Black-headed Gulls (*Croicephalus ridibundus*) in Europe. For example, in Kalmar, Sweden an ongoing outbreak has resulted in the deaths of a substantial number of adults and nearly all juveniles across 5 breeding colonies from June–July, 2023 (pers. comm. Waldenström), reports have also suggested more than 2,000 dead gulls reported in the Netherlands (DWHC 2023), > 10,000 have died in the UK (BirdGuides 2023), and outbreaks have also been reported in France, Belgium, Germany and Lithuania. Other colony-breeding seabirds affected include Black-legged Kittiwakes (*Rissa tridactyla*), with 12,000 dead Kittiwakes reported in northern Norway (WAHIS 2023), and auks across Europe. Early outbreaks of HPAI in South America were heavily skewed towards pelicans and cormorants, rather than waterfowl. Approximately 41% of all Peruvian Pelicans (*Pelecanus thagus*) are believed to have died in a matter of weeks in early 2023. A similar number of Guanay Cormorant (*Leucocarbo bougainvillei*, $n = 26,105$) and Peruvian Boobie (*Sula variegata*, $n = 53,034$) carcasses were also reported in Peru in February (Ariyama *et al.* 2023; Leguia *et al.* 2023). Currently, it is believed that > 500,000 wild birds have died in South America (up till July 2023). Finally, often neglected in the HPAI narrative is southern Africa, where devastating outbreaks have occurred since ~2017. Of great concern is the impact on African Penguins (*Spheniscus demersus*); between December 2018 and February 2019 more than 350 African Penguins (~5% of the colony) died in Namibia (Molini *et al.* 2020), and in 2022 a further 230 penguins died in South Africa (Reuters 2022). This projects a terrible future for penguins if HPAI enters Antarctica.

To date, HPAI has been detected in a large diversity of carnivores and scavengers including members of Canidae (5 species),

Mustelidae (10 species), Felidae (7 species), Procyonidae (2 species), Mephitidae (1 species), Ursidae (4 species), and Didelphidae (1 species) (European Food Safety Authority, *et al.* 2023). These animals are likely being directly infected by the consumption of sick or dead wild birds (e.g., Tammiranta *et al.* 2023), so cases are sporadic, and are tied to locations where there are large numbers of bird carcasses in the environment. Of substantial concern are detections in marine mammals, including members of the Phocoenidae (2 species), Delphinidae (4 species), Otariidae (2 species), and Phocidae (3 species) (European Food Safety Authority, *et al.* 2023). Of note are the > 20,000 South American Sea lions (*Otaria flavescens*) reported dead in Chile and Peru, comprising ~9% of the regional population (Chile Servicio Nacional de Pesca y Acuicultura 2023; Peru Ministerio de Salud 2023), which comprises a major deviation from the low numbers seen in most affected mammalian species. As such, HPAI may pose a substantial conservation concern to marine mammals.

As these examples testify, the HPAI panzootic has clear conservation and ecological implications. HPAI has already impacted threatened species, such as African Penguins (Endangered), undoing decades of conservation gains. And there are many more endangered species, from waterbirds to raptors, where an HPAI outbreak could significantly affect population numbers, contributing to increased extinction risks. The mortalities in less vulnerable species are just as concerning due to the sheer scale. Many affected waterbird species are long-lived and whose life histories depend on high annual survival such that the large-scale loss of breeding adults has the potential for significant impacts at a population and species level. Large scale “removal” of avian species from the environment through mass mortality events could have large ecosystem level effects as waterbirds have diverse roles ranging from predation and herbivory to seed dispersal.

While waterbirds are undoubtedly being heavily affected by HPAI, they are also contributing to virus spread, both on local and long-distance scales. Not all individuals in-

ected with HPAI die (e.g. Lane *et al.* 2023), and different species respond differently to infection, with some species showing no or limited clinical signs of disease, such as *Anas* duck populations (Poen *et al.* 2018). That Mallards have few disease signs has been confirmed in experimental studies, whereby 58% of Mallards not only survived infection, but had no observable disease signs (Spackman *et al.* 2023). Further, infected Mallards may migrate despite infection, demonstrated by satellite tracked individuals (Lv *et al.* 2022). The ability of some birds to not only withstand infection, but to have subclinical infections and therefore spread HPAI silently poses an enormous challenge for HPAI mitigation efforts.

How to Weather the Storm?

The outbreaks of HPAI will no doubt have a lasting impact on waterbirds, especially for long-lived species such as terns, skuas, gannets and pelicans which have experienced substantial mass mortality of breeding populations. While interventions against HPAI in poultry are straightforward (although not easy), mass culling or vaccination of waterbirds is not a feasible path forward (CMS FAO Co-convened Scientific Task Force on Avian Influenza and Wild Birds 2023), despite having been proposed in special cases. Available actions for the control of HPAI in waterbirds largely revolve around prevention of viral spillover from poultry to waterbirds, surveillance in waterbirds, appropriate outbreak response, and protection of species/populations with high conservation concern.

First, despite the clear role of waterbirds in this panzootic, HPAI viruses are still continually seeded from poultry. As such, decreasing the viral loads in poultry, decreasing the number of outbreaks in poultry, and prevention of viral escape from poultry via stricter biosecurity is therefore critical. Second, comprehensive water bird surveillance systems are important, but presently are largely funded and designed as an early warning system for poultry. However, if designed appropriately, surveillance systems

may also provide critical information pertaining to ecology of this virus - as well as that of other pathogens. That is, we may reveal which species play roles as reservoirs (hosts that maintain viruses), dead-end spillover hosts (hosts that are only occasionally infected and don't contribute to long term circulation), and factors such as seasonality, role of immunity etc. These data may then be combined with movement ecology, leveraging the increasing number of birds followed by telemetric devices to identify areas of breeding overlap, routes of migration, habitat use as well as speed of migration (van Toor *et al.* 2018; Waldenström *et al.* 2022). Arguably, however, waterbird surveillance should also benefit waterbirds, particularly in the current panzootic wherein we are seeing population and species level effects. In response, we may be able to direct interventions at wild bird populations or species, such as the proposed vaccination campaign of California Condors (*Gymnogyps californianus*; Kozlov 2023). Third, following an outbreak, data on outbreak parameters are critical. A key feature of all HPAI outbreaks to date is the prioritization of response towards poultry, such that there is almost no, or limited information pertaining to waterbird outbreaks. For example, of the ~20,000 Sandwich Terns reported in (Knief, *et al.* 2023), only 68 were reported to the World Organisation for Animal Health (Klaassen and Wille 2023). Mortality data from wild bird outbreaks are critical for population assessments, conservation plans, International Union for Conservation of Nature (IUCN) status etc, so this mismatch between reports from the ground and notifications to the most comprehensive database is highly concerning. A ramification of surveillance programs not designed for the benefit of waterbirds are the large geographic "black boxes" on the global scale. In some regions there is rapid and comprehensive release of data, pre-prints and publications with short timeframes from heavily affected areas, such as Peru and Chile (e.g., Chile Servicio Nacional de Pesca y Acuicultura 2023; Gamarra-Toledo *et al.* 2023). Not only does this increase our general understanding of the scale and ramification of

the outbreaks which have occurred there, this is of direct benefit to neighbouring countries in their preparation activities. In other regions, particularly in Asia, we have numerous areas with no or few reported wild bird outbreaks directly adjacent to areas reporting substantial outbreaks (e.g., Japan, or South Korea), such that the situation is unclear. HPAI is clearly a global problem, and requires global cooperation, timely data sharing, improved and standardised recording systems for wildlife settings, greater virus phylogenetic analyses, good population monitoring and research efforts (CMS FAO Co-convended Scientific Task Force on Avian Influenza and Wild Birds 2023). While there is a substantial drive to tackle issues around infectious and emerging diseases in a One-Health framework (the combined consideration of environmental, animal and human health), the reality remains that vastly more money and resources are directed to human health, followed by food-producing animal health given the socioeconomic status.

Despite the devastation, we should not lose hope. Through heavy losses at colonies, tracking studies detected prospecting behaviour in adult Northern Gannets. While this behaviour may have contributed to disease spread through increased contact between colonies, we may be seeing behaviour to decrease exposure to disease (Jeglinski *et al.* 2023). Individuals remaining in populations following outbreaks may be more resistant to infection, i.e., are better able to clear the infection than non-resistant hosts. For example, as a result of the *Mycoplasma gallisepticum* epizootic in North American House Finches, surviving individuals and populations are resistant to *Mycoplasma* infection (Bonneaud *et al.* 2019). Studies addressing preexposure of avian influenza have demonstrated that Mallards exposed to LPAI have fewer clinical signs when infected with HPAI compared to those that do not (Tarasiuk *et al.* 2023), which may be a key reason as to why infected Mallards have few disease signs and are able to migrate while infected. Further, long lived species, such as seabirds may retain antibodies for many years, such that both previous LPAI or HPAI infection will be

protective (Ramos *et al.* 2014). However, the influenza A virus is notorious for high variability and rapid evolutionary rates which allows for virus escape from resistant individuals with time. This, in combination with high recruitment of immunologically naive juveniles into the population, may be one explanation as to why waterbird populations in Europe continue to be heavily infected, despite repeated waves of clade 2.3.4.4 HPAI since 2014.

Overall, the HPAI panzootic is far from over. We call on policy makers to consider and protect waterbirds through measures such as proactively designed systems to protect waterbirds and to respond to waterbird outbreaks (e.g., Pearce-Higgins *et al.* 2022). While outbreaks in poultry have enormous socio-economic costs and require rapid short-term responses, the loss of waterbirds at this scale will likely be not only a conservation disaster, but also an ecological disaster, and therefore outbreaks in wild birds must be prioritized.

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