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Feathers and flu: identifying data gaps in avian influenza host dynamics to prioritize wildlife conservation

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Abstract

Highly pathogenic avian influenza viruses (HPAIV) have had disastrous, worldwide effects on wild birds and domestic poultry since the emergence of the A/goose/Guangdong/1/1996 (Gs/GD/96) lineage. The currently circulating H5N1 clade 2.3.4.4b has an expanded set of susceptible hosts, including many migratory wild birds, and is associated with higher transmission rates, increased susceptibility among wild bird hosts, and a greater number of wildlife reservoirs. Certain wild bird life-history strategies and behaviors have been suggested to explain avian hosts' susceptibility and exposure to HPAIV. These biological traits include gregariousness, such as colonial nesting and mixed flock foraging, predation or scavenging on wild birds, and association with aquatic habitats. Variation in host infection responses (e.g., infectability, shedding rates and duration, mortality rate, antibody development) informs the overall infection risk across avian species, yet the specific role of biological traits is often inconsistent and unclear across taxa. Moreover, the interactions and potential compounding effects among these biological traits remain

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largely unknown. To develop a more holistic understanding of cumulative risk across bird species, we integrate existing information on infection risk factors (i.e., susceptibility, immunological response, and behavioral traits) into a qualitative multivariate analysis. This approach enabled us to examine how infection risk factors relate to biological traits (e.g., phylogeny, physiology, behavior, species range) and to begin disentangling their complex interactions. We quantified and summarized these risk factors across host species and qualitatively ranked species by their viral responses along a proposed HPAIV response continuum, guided by expectations of traits and metrics associated with competence or vulnerability to HPAIV. In doing so, we aimed to better understand how viral responses and biological traits synergistically interact to influence cumulative risk across wild bird species. This work broadly expands on the previous avian influenza literature, which has focused on Anseriformes and Charadriiformes as primary viral reservoirs. We tie our findings to effective disease management responses with links to risk components, including descriptions of potential surveillance strategies applied to research and One Health goals, as well as a fuller understanding of how resources may be better deployed for rapid response when spillovers do inevitably occur. Additionally, we identified numerous areas where vital epidemiological information is lacking to best characterize the spread of these viruses. Ultimately, this improved understanding will help identify and inform disease management needs and decision making.

KEYWORDS
avian ecology, avian influenza, disease risk, H5Nx, host competence, One Health, policymaking, spillover, susceptibility, zoonotic disease

Resumen

Los virus de la influenza aviar altamente patógena (HPAIV) han tenido efectos desastrosos a nivel mundial en las aves silvestres y las aves de corral desde la aparición del linaje A/ganso/Guangdong/1/1996 (Gs/GD/96). El clado H5N1 2.3.4.4b, que circula actualmente, tiene un conjunto ampliado de huéspedes susceptibles, incluidas muchas aves silvestres migratorias, y está asociado con mayores tasas de transmisión, mayor susceptibilidad entre los huéspedes de aves silvestres y un mayor número de

reservorios de vida silvestre. Se ha sugerido que ciertas estrategias y comportamientos de la historia de vida de las aves silvestres explican la susceptibilidad y la exposición de los huéspedes aviares al HPAIV. Estos rasgos biológicos incluyen la gregarismo, como la anidación colonial y la búsqueda de alimento en bandadas mixtas, la depredación o el carroñeo de aves silvestres y la asociación con hábitats acuáticos. La variación en las respuestas a la infección del huésped (por ejemplo, infectividad, tasas y duración de la excreción viral, tasa de mortalidad, desarrollo de anticuerpos) influye en el riesgo general de infección en las especies de aves; sin embargo, el papel específico de los rasgos biológicos suele ser inconsistente y poco claro entre los taxones. Además, las interacciones y los posibles efectos combinados entre estos rasgos biológicos siguen siendo en gran medida desconocidos. Para desarrollar una comprensión más integral del riesgo acumulativo en las especies de aves, integramos la información existente sobre los factores de riesgo de infección (es decir, susceptibilidad, respuesta inmunológica y rasgos conductuales) en un análisis multivariado cualitativo. Este enfoque nos permitió examinar cómo se relacionan los factores de riesgo de infección con los rasgos biológicos (por ejemplo, filogenia, fisiología, comportamiento, distribución de la especie) y comenzar a desentrañar sus complejas interacciones. Cuantificamos y resumimos estos factores de riesgo en las especies huésped y clasificamos cualitativamente las especies según sus respuestas virales a lo largo de un “continuo de respuesta al HPAIV” propuesto, guiados por las expectativas de los rasgos y las métricas asociadas con la competencia o la vulnerabilidad al HPAIV. Al hacerlo, nuestro objetivo fue comprender mejor cómo las respuestas virales y los rasgos biológicos interactúan sinérgicamente para influir en el riesgo acumulativo en las especies de aves silvestres. Este trabajo amplía la literatura previa sobre la influenza aviar, que se ha centrado en los Anseriformes y Charadriiformes como principales reservorios virales. Vinculamos nuestros hallazgos con respuestas efectivas de gestión de enfermedades con enlaces a los componentes de riesgo, incluidas descripciones de posibles estrategias de vigilancia aplicadas a la investigación y los objetivos de Una Salud, así como una comprensión más completa de cómo se pueden implementar mejor los recursos para una respuesta rápida cuando inevitablemente se producen

desbordamientos. Además, identificamos numerosas áreas donde falta información epidemiológica vital para caracterizar mejor la propagación de estos virus. En definitiva, esta mejor comprensión ayudará a identificar y a orientar las necesidades de gestión de enfermedades y la toma de decisiones.

Contents

INTRODUCTION

Over the past 20 years, highly pathogenic avian influenza viruses (HPAIV) have increasingly affected wild bird populations, domestic poultry production, and public health. The currently circulating strain of H5N1 clade 2.3.4.4b has resulted in the largest globally distributed panzootic event, characterized by rapid global spread, efficient transmission to new bird species (Xie et al. 2023), spillover to mammals (Elsmo et al. 2023, Burrough et al. 2024), and changes in seasonal and annual viral circulation in wild birds (Harvey et al. 2023, Stallknecht et al. 2024). The epicenter of HPAIV has now shifted outside of Asia, with Europe and the Americas emerging as pivotal nodes in transmission and dispersal. The magnitude and spread of HPAIV panzootic transmission have introduced a novel stressor to bird species already facing severe population declines due to the cumulative effects of climate change, habitat loss and degradation, food stress, contaminant exposure, and other emerging pathogens (Croxall et al. 2012, Rosenberg et al. 2019). This represents a conservation crisis for wild birds, particularly waterbirds and raptors, which are the avian taxa predominantly impacted by HPAIV mortality (Wille and Waldenström 2023, Avery-Gomm et al. 2024). Despite this ongoing crisis, we are still limited in species-specific epidemiological information across avian hosts.

Highly pathogenic avian influenza virus evolution

Influenza A viruses (IAV) are globally distributed pathogens that infect a broad range of host species, most commonly birds, mammals, and notably humans. Strains that have historically impacted birds are broadly referred to as avian influenza viruses (AIV) and are classified as either low or highly pathogenic (LP, HP), a definition based on their ability to cause high mortality in chickens (van der Goot et al. 2003) or the presence of specific mutations in the hemagglutinin (HA) surface glycoprotein. Of AIV, H5Nx highly pathogenic avian influenza viruses (HPAIV) are particularly important zoonotic pathogens, with ecological origins in aquatic birds, where most of the HPAIV diversity circulates. Historically, most circulating strains have been low pathogenic avian influenza viruses (LPAIV), which cause mild or subclinical infections in Anseriformes (i.e., ducks, geese, and swans) and certain Charadriiformes (i.e., gulls, terns, and shorebirds), the historical natural reservoirs and co-evolved hosts (Sonnberg et al. 2013).

Shifts in viral strains have driven substantial changes in viral system dynamics (Supplemental 1: A Global Timeline of HPAIV H5 Transmission in Wild Hosts, available in Supporting Information). The H5N1 viruses currently circulating in the United States descend from the Eurasian genetic clade 2.3.4.4b of the Gs/GD/96 lineage, which originated in Guangdong Province, China, in 1996 and subsequently spread and diversified across Eurasia before being introduced into North America (Caliendo et al. 2022b, Xie et al. 2023). The recent HPAIV H5N1 strains have had severe impacts in the United States, affecting 3.64 million poultry and contributing to wild bird mortality across 141 species, many of which were previously not known to be susceptible (U.S. Department of Agriculture Animal and Plant Health Inspection Service [USDA APHIS] 2024a, b). Spillover into mammals has also expanded, with detections in 27 wild and domestic mammalian species in the United States, including 2 confirmed spillovers into dairy cattle, which subsequently led to over 800 farm-to-farm transmission events across 16 states, and infections in small mammals, domestic cats, and dogs at farms where outbreaks occurred (USDA APHIS 2024c, d). Such developments elevate concerns of zoonotic spillover, viral adaptation, and pandemic potential, particularly as increasing human infections have been documented (Garg et al. 2024, Centers for Disease Control and Prevention

[CDC] 2025, Wang et al. 2025). The increased adaptation of HPAIV H5Nx to be maintained by migratory wild birds (James et al. 2023, Xie et al. 2023) has driven the recent geographical expansion and persistence of the virus. Consequently, understanding the host responses of migratory wild birds to infections is essential to our understanding of viral transmission and geographical dissemination of HPAIV.

The segmented genome of the influenza A viruses enables genetic reassortment (i.e., exchange of the virus's 8 gene segments) when host cells are co-infected with multiple strains. Reassortments can then lead to antigenic shift, producing new viral genotypes with altered antigenic properties that can enable immune evasion (Smith et al. 2009). Reassortment and mutation are central to IAV evolution, generating diversity in infectivity, pathogenesis, and host range among HPAIV H5Nx (Zhou et al. 2009, Charostad et al. 2023). Prior to the early 2000s, HPAIV outbreaks in wild birds were rare, and the Gs/GD/96 lineage was largely maintained within domestic birds. Following the initial spillover into wild birds and the large-scale mortality event at Qinghai Lake in 2005, reassortant viruses were increasingly detected during transmission from domestic to wild birds (Li et al. 2010, Zhao et al. 2012, Fan et al. 2014), with increasing detections of wild birds facilitating HPAIV through migratory flyways (Prosser et al. 2011, Fourment et al. 2017, Blagodatski et al. 2021). Despite repeated reassortment and genetic drift between 2002 and 2020 producing extensive diversification within the Gs/GD/96 lineage, long-term persistence in wild bird populations remained limited. This pattern shifted with the emergence of clade 2.3.4.4b H5Nx, which has exceeded earlier lineages in prevalence, host breadth, and geographic spread, and now shows clear evidence of sustained circulation and dissemination via wild bird migratory movements (Figure 1).

HPAIV in wild populations – migratory, demographic, and seasonal drivers

The spread and persistence of HPAIV clade 2.3.4.4b in the United States are closely linked to the expanding host range of the virus, host demographics, and seasonal migratory behaviors (Gass et al. 2023b, Teitelbaum et al. 2023b, Damodaran et al. 2025, Sullivan et al. 2025a). Breeding, staging, and wintering sites characterized by high bird abundance can facilitate the transmission of IAVs and serve as reservoirs of genetic diversity and reassortment. Seasonal patterns of avian reproduction and migration play a central role in IAV transport and transmission (Yang et al. 2024), and the timing of avian reproduction and migrations play a critical role in the transport and transmission of IAVs, including HPAIV. Autumn is well documented as a peak period for IAV prevalence in wild birds, largely driven by the influx of immunologically naive juveniles into populations (Olsen et al. 2006, Munster and Fouchier 2009, Hénaux et al. 2010, Nolting et al. 2018, Gorsich et al. 2021). High susceptibility of naive juveniles along with mixing of individuals of different ages and from different breeding grounds amplifies transmission during pre-migratory staging and migration (Garnier et al. 2011, Dirsmith et al. 2018, Ineson et al. 2022, Wille et al. 2023). As birds age and acquire immunity, prevalence generally declines, explaining the reduced infection rates during winter and spring (Hénaux et al. 2010, Hill et al. 2012, Nallar et al. 2015, Kent et al. 2022). Despite this typical seasonal pattern, smaller peaks in late winter and early spring have been observed and may contribute to persistence and year-round circulation of local viruses (Kent et al. 2022). Drivers of non-autumnal increases are potentially many (Kent et al. 2022), including changes in circulating subtypes (Diskin et al. 2020), an influx of migratory individuals that amplify transmission (Verhagen et al. 2014), physiological stress, increased gregariousness, and interspecies mixing during migration (Hill et al. 2016, Moore 2018, Cohen et al. 2021).

Unlike previous HPAIV H5Nx outbreaks, the timing of the initial 2021 North American incursion resulted in unusually high detections in and mortality of wild birds during the typically low transmission spring and summer periods, with sustained viral transmission throughout the year (Harvey et al. 2023). This pattern was likely driven by widespread immunological naivety across wild bird taxa. In subsequent years, some populations began to exhibit more stable seasonal patterns (Stallknecht et al. 2024) as is common with endemic LPAIVs. Spatial analyses showed elevated HPAIV prevalence in the fall and winter in the Pacific Northwest and Great Lakes regions (Gorsich et al. 2021, Kent et al. 2022), 2 major areas of waterfowl aggregation, post-breeding (Davis et al. 2014). As birds migrate south during the fall, many high-density stopover locations are concentrated throughout the southern

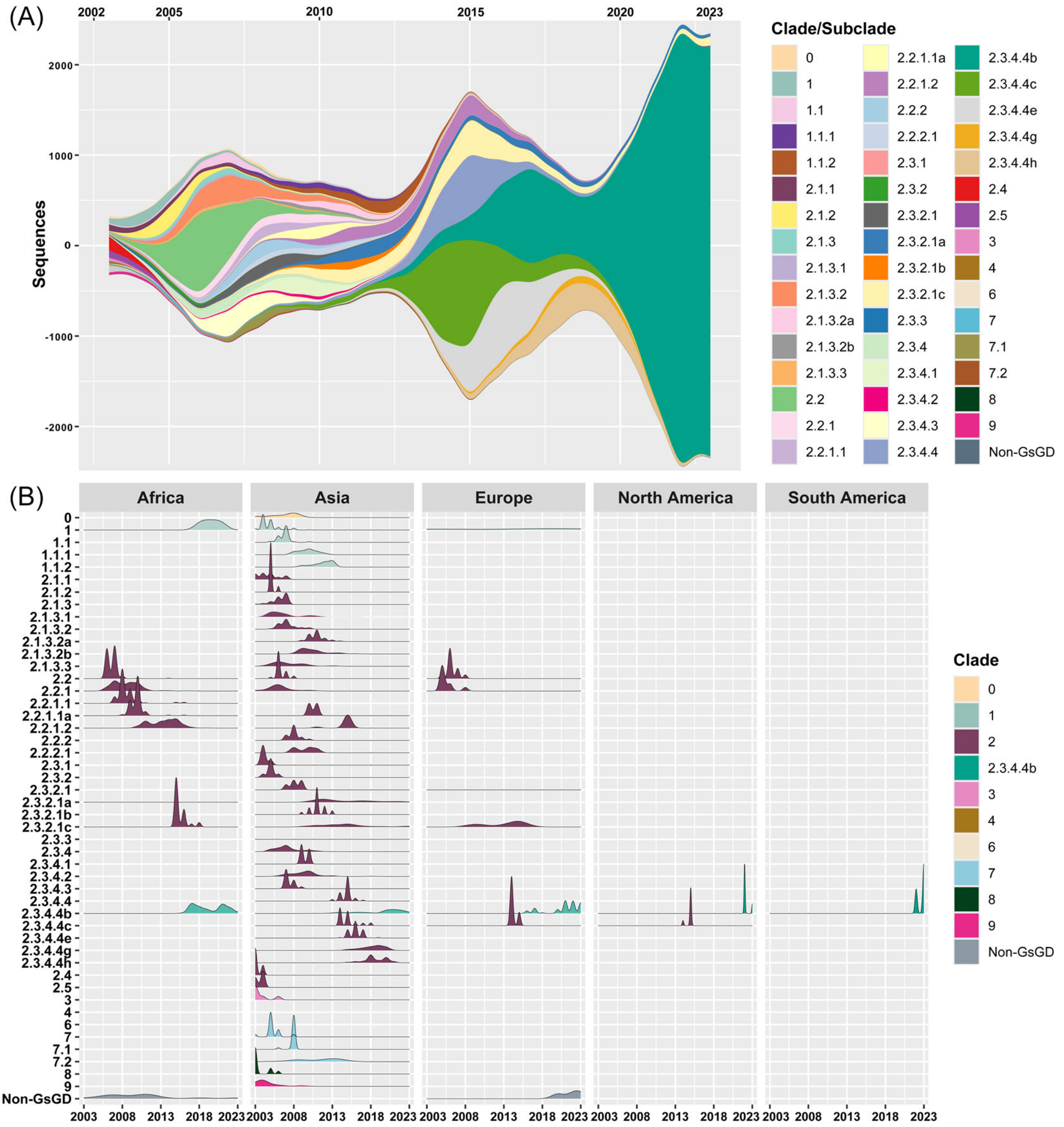

FIGURE 1 Timelines from 2003 to 2023 of sequences and their clade or subclade designations for all highly pathogenic avian influenza viruses (HPAIV), including Gs/GD and non-Gs/GD data, submitted to the Global Initiative on Sharing All Influenza Data (GISAID) EpiFlu$^{\mathrm{TM}}$ database (Elbe and Buckland-Merrett 2017) as plotted by collection date. A) Timeline of worldwide clade or subclade sequence frequencies, demonstrating the rapid proliferation of viral diversity and how it has come to be dominated by subclade 2.3.4.4b. B) Timeline of clade or subclade frequencies across world regions, demonstrating the historical epicenter in Asia and the shift to Africa, Europe, North America, and South America. Antarctica was excluded from the figure because of the limited number of detections occurring by the end of 2023 (*n* = 3).

United States (La Sorte et al. 2014). However, data gaps in IAV sampling across the annual cycle remain for many species, limiting a comprehensive understanding of these seasonal patterns (Nolting et al. 2018, Kent et al. 2022).

In North America, migratory corridors facilitate viral gene flow both intra- and inter-continentally (Pearce et al. 2011, Fourment et al. 2017, Caliendo et al. 2022b). Approximately 73% of breeding birds in North America are migratory, resulting in billions of potential hosts moving across the continent annually, while 54% undertake long-distance migrations to Central and South America (Albert et al. 2020). Additional inter-continental migrations occur via the Atlantic (via Canada, Greenland, and Iceland) or Pacific Ocean (via Alaska and Bering Strait), providing potential pathways for long-distance IAV dispersal (Pearce et al. 2009, Dusek et al. 2014, Wille et al. 2014, Alkie et al. 2022). Virus dispersal by migratory birds, both within and less frequently across flyways, has facilitated the rapid cross-continental spread of H5N1 viruses, as evidenced by detection of HPAIV clade 2.3.4.4b across all 4 North American flyways within 4.8 months of the initial 2021 incursion (Damodaran et al. 2025).

Long-term surveillance of LPAIVs in wild avian populations over multiple decades identified 16 (H1-16) of the 19 known hemagglutinin (HA) subtypes (H19 has been genetically detected but not isolated, hence considered unconfirmed (Karakus et al. 2024), with subtype diversity varying across taxonomic groups (Yin et al. 2023). Waterfowl, in particular, act as reservoirs for the majority of HA subtypes, with H3, H4, and H6 being most frequently detected (Krauss et al. 2004, Diskin et al. 2020, Prosser et al. 2022). In contrast, non-waterfowl aquatic birds within the order Charadriiformes are primary hosts for other subtypes, notably H13 and H16 in gulls (Laridae; Munster and Fouchier 2009) and H12 and H13 in shorebirds (Poulson et al. 2020). Subtypes H5 and H7 have been detected across these major avian groups, with some species acting as reservoir hosts (e.g., LP H5, H7 in some shorebirds and waterfowl), while others are more commonly associated with outbreak events (e.g., HP H5 in gulls and waterfowl). Phylogenetic analyses have demonstrated that a broad range of avian hosts contribute to the global dissemination of IAVs in different ways. For example, gulls have been shown to contribute to rapid transoceanic spread of HPAIV H5, while wild ducks facilitate swift regional dispersal and geographic expansion (Hill et al. 2022). The interplay between wild bird migratory ecology and virus tropism is key to the expanding state of clade 2.3.4.4b in the United States and globally.

Immunological response in wild birds

The diversity of hosts and scale of bird mortality events attributed to HPAIV (Scientific Task Force on Avian Influenza and Wild Birds 2022, Gamarra-Toledo et al. 2023, Avery-Gomm et al. 2024) underscore a critical need to deepen our understanding of the immunological responses of wild birds and identify host adaptations that are associated with decreased mortality rates. Our understanding of wild bird host immune response to IAVs is based primarily on challenge (i.e., experimental infection) studies and survival data, the latter of which is limited to intensively monitored species such as northern gannets (*Morus bassanus*; Lane et al. 2024, Lewis et al. 2026). A limited number of studies have sought to identify the distinct immune pathways and proteins associated with recovery or tolerance of AIVs (Dolinski et al. 2022a, b). By understanding how immunological responses and host response phenotypes vary across species, we can better identify differences in infection tolerance that shape both host survival outcomes and potential roles in viral transmission.

The variation in immunocompetence (Box 1) plays a key role in shaping viral outbreak dynamics and varies by host species, population, age, sex, and season. Peaks in HPAIV activity often coincide with periods of immunological naivety as young-of-year birds enter the population. Nestlings have partially developed immune systems, though this varies in altricial versus precocial birds, and receive protection from maternal antibodies. Their adaptive immunity continues to develop for several weeks after hatching (Härtle et al. 2014), creating a window of heightened susceptibility that coincides with pre-migration staging (Gass et al. 2023b). Juvenile birds are particularly vulnerable to AIV owing to the lack of prior infection and the waning of maternal antibodies (Boulinier and Staszewski 2008, Lamb et al. 2024), where immunity is less robust than that of adults (Hudson and Dobson 1997, Hill et al. 2016). Field surveillance studies demonstrate that juveniles generally exhibit higher infection prevalence (van Dijk et al. 2014, Nallar et al. 2016, Papp et al. 2017), increased viral shedding (Costa et al. 2010, Jourdain et al. 2010, Hoye et al. 2012, van Dijk et al. 2014), and lower serum antibody prevalence (Hoye et al. 2012, Tolf et al. 2013, van Dijk et al. 2014, Nallar et al. 2016, Hill et al. 2016) compared to adults, although exceptions exist (Teitelbaum et al. 2023b). Subtle sex differences in wild bird immunity have been suggested. Such differences are likely influenced by species-specific differences along with breeding, season, age, and associated stressors that can affect immunosuppression (Hill et al. 2016, Valdebenito et al. 2021).

BOX 1. Glossary: Definitions for terminology implemented in text as it applies to Influenza A viruses, including A) disease ecology and host-virus interactions, B) host-mediated transmission roles, and C) viral classification.

A. ***Disease Ecology and Host-virus Interactions***

Competence: propensity of a host to transmit virus and infect other hosts (Kuiken et al. 2006, Martin et al. 2016).

Dispersal: geographic spread of virus.

Immunocompetence: a host's ability to mount an effective immune response. In birds, mediated by individuals' innate (i.e., non-specific) and adaptive (i.e., cell-mediated response by lymphocytes and macrophages and humoral response involving antibodies) immune systems.

Life-history strategies: characteristics of a species to optimize survival and reproduction, including behaviors and ecological roles. These include gregariousness, movement patterns, habitat preferences, and feeding strategies that shape how a species interacts with its environment and other species.

Reservoir: a host species capable of sustained maintenance of the virus and serving as the source of infection for other hosts (Haydon et al. 2002).

Shedding: the release of virus from an infected individual into the environment.

Species-level infection metrics: quantifiable indicators of how an individual reacts to infection, including infection rate, shedding rates, duration of shedding, mortality rates, and prevalence of immunity (antibody protection) following infection.

Spillback: transmission of virus from novel host back to original hosts.

Spillover: transmission of virus from an original host to a novel host.

Susceptibility: reflects likelihood of the host being infected upon exposure to a virus, determined by the host's biology, physiology, and immune status (Altizer et al. 2011, Gervasi et al. 2017, van Seventer and Hochberg 2017, Downs et al. 2019, Martin et al. 2019, Z. Y. X. Huang et al. 2023).

Tolerance: the ability of a host to minimize the costs of infection for a given viral burden by limiting or repairing host damage without negatively affecting virus fitness (Råberg et al. 2007, Adelman and Hawley 2017, Downs et al. 2019).

Transmission: movement of virus from one host to another either directly (host to host) or via the environment.

Virulence: descriptor for the harm caused by viral infection, particularly in terms of host morbidity and mortality (Geoghegan and Holmes 2018).

Vulnerability: incorporation of susceptibility along with environmental and social determinants that inform the probability of mortality when the host is infected (i.e., risk of mortality; Stephen 2014, Gervasi et al. 2017).

B. ***Host-mediated transmission roles*** **("super" roles have been adapted from** Martin et al. 2019 **and describe extremes of the given response mode)**

HPAIV host response continuum: a conceptual characterization describing the range of host responses to HPAIV exposure and infection, across different host species or individuals. The continuum is informed by 2 primary axes, host competence and vulnerability, which together inform the potential for extreme host roles and contributions to HPAIV amplification, transmission potential, and epidemiological outcomes.

Superconsumer: a host that consumes virus through scavenging and hunting of infected prey.

Superdiluter: a host that is less susceptible than other hosts, can "dilute" transmission through several potential mechanisms, including by reduced host contact, reduced transmission probability, reduced susceptible or infected host abundance, and increased mortality of infected individuals (Keesing et al. 2006).

Supermover: a host that can disperse virus long distances through movement, presumably mediated by high competence and low vulnerability.

Superreceiver: a host that is highly exposed to virus, through contact with infected individuals, environmental exposure, or through other behaviors.

Supershedder: a host that releases a large amount of virus into the environment.

Superspreader: a host that increases exposure and infection risk to others.

C. ***Classifying avian influenza A virus***

Clade: refers to closely related phylogenetic group of strains that form a monophyletic cluster (i.e., an ancestor and all its descendants). The Gs/GD/96 phylogeny has been designated into second- to fifth-order subclades.

Lineage: a broad category that refers to a genetically distinct group that shares a common ancestor. Lineages are identified by similarity in their genetic sequence that reflects their evolutionary relationship. For example, the A/goose/Guangdong/1/1996 lineage, commonly referred to as the Goose/Guangdong/96 (Gs/GD/96) lineage, includes all descendants of the originator strain.

Strain: refers to the specific genetic and phenotypic variant that was detected, isolated, and sequenced, independent of the context of ancestors or descendants. Distinct strains can vary by small numbers of mutations in their genetic sequence, changes in pathogenesis, transmissibility, or geographic and temporal distribution. When strains are identified, they are labeled following a naming convention of providing the influenza type, species isolated from, location detected, and a unique identifier for the strain number, year, and subtype. Resulting in names such as A/goose/Guangdong/1/96 (H5N1).

Subtype: characterized based on the composition of hemagglutinin (HA) and neuraminidase (NA) surface proteins, which result in distinct subtype combinations (e.g., H5N8, H7N3; described in further detail in Supplemental 1: A Global Timeline of HPAIV H5Nx Transmission in Wild Hosts, available in Supporting Information), such as the H5N1 subtype of current concern.

Challenge studies in wild bird species

Understanding variability in host response to IAV can enhance immunological studies, inform models of viral dynamics, and provide evidence-based insights that can inform surveillance strategies and response planning. Knowledge of viral shedding and movement can be used to identify key species in transmission dynamics (Breban et al. 2009, Hénaux and Samuel 2011; see Supplemental 2: Migratory Connectivity and HPAI), but infection dynamics can vary with viral lineage (Fuller et al. 2010) and across populations (Avery-Gomm et al. 2024). As viral response is difficult to describe from wild free-ranging animals, researchers rely on experimental infection studies conducted in laboratory settings to assess host infection responses throughout the period of infection. While such studies are intended to control for environmental variables, individual viral response may still be influenced by the method of infection (e.g., inoculation versus contact), infectious dose, and individual heterogeneity, suggesting that consideration must be taken when comparing responses across challenge studies (Gonnerman et al. 2024). For example, the infectious dose (e.g., amount of virus required to infect inoculated embryo eggs, such as 50% embryo infectious dose [EID] or EID_{50}) used to inoculate animals will affect infectivity, mortality, and shedding response. Similarly, animals may be either immunologically naive or have been previously infected with an IAV when exposed to a virus for a study, which may alter susceptibility and capacity to shed. Researchers can inoculate animals with multiple viruses, such as an LPAIV strain prior to exposure with an HPAIV strain (Berhane et al. 2010, Costa et al. 2011, Hiono et al. 2016, Caliendo et al. 2022b), to emulate natural protections from prior infections of LPAIs or non-Gs/GD lineages, which can result in cross-reactive antibodies and protective immunity (Caliendo et al. 2022a).

The literature describing wild bird responses to AIV exposure and infection remains sparse and uneven, given the growing number of species now known to be affected. As of 1 March 2024, only 28 species, across 104 published studies, have been included in experimental studies (Gonnerman et al. 2024), despite confirmed HPAIV infections across 167 wild bird species in the United States (U.S. Geological Survey National Wildlife Health Center 2021, USDA APHIS 2024b; Figure 2).

Many marine and coastal birds are colonial nesters, breeding in dense colonies that can facilitate rapid viral transmission (Clancy et al. 2006, Knief et al. 2023). Outside of Anseriformes hosts, IAVs are highly adapted to Charadriiformes such as gulls, terns, and shorebirds. When considering other groups of concern for their driving roles in IAV and HPAIV disease dynamics, gulls are of increased concern due to their large abundances, wide distributions, and adaptation to living near humans (Hill et al. 2022). Of the gull species found in the United States, only laughing (*Leucophaeus atricilla*), herring (*Larus smithsonianus*), and black-headed gulls (*Chroicocephalus ridibundus*) had available challenge data. These species exhibited low to moderate shedding rates with extended shedding durations (Ramis et al. 2014, Tarasiuk et al. 2022), and in the case of laughing gulls, lower mortality (Perkins and Swayne 2002, Brown et al. 2006). Coupled with their broad movement capacity (Enners et al. 2018, Anderson et al. 2020), these traits suggest gulls could act as long-distance facilitators of viral dispersal (Hill et al. 2022).

Aside from studies on gulls and a single experiment on black-crowned night herons (*Nycticorax nycticorax*; Soda et al. 2022b), there is a lack of comparable experimental data on colonial-nesting waterbirds or marine birds from the United States. This represents a notable knowledge gap, but not one that can or should be addressed through challenge studies across all affected species, many of which are declining, of conservation concern, or logistically unsuitable for such work. Instead, these gaps highlight the need for carefully targeted research efforts, whether experimental, field-based, or model-driven efforts, focused on species for which approaches are feasible, ethically justified, and capable of yielding relevant insights.

Several avian families recently shown to be susceptible to HPAIV, such as Gruidae, Pelecanidae, Spheniscidae, and Sulidae (Barriga et al. 2016, Gamarra-Toledo et al. 2023, Knief et al. 2023, Avery-Gomm et al. 2024), warrant consideration in this context. For example, several crane species globally have experienced infections (Yang et al. 2023) and notable mortality events (Scientific Task Force on Avian Influenza and Wild Birds 2022), including a sandhill crane (*Grus canadensis*) mass mortality event in the Central Flyway of the United States in early 2025 and 2 mortality detections of whooping cranes (*Grus americana*) in southern Saskatchewan in October 2025 (Canadian Food Inspection Agency National Emergency Operations Center, Geographic Information System Services 2025). These events indicate a need for further understanding of susceptibility and immune responses in North America's native cranes. Given their long-distance migrations, large seasonal aggregations, and extensive mixing with other species at stopover sites (Krapu et al. 2014), carefully designed research may provide valuable context for assessing disease responses and putative host roles.

Raptors and scavenging birds may experience increased exposure risks through predation or scavenging on infected animals (van den Brand et al. 2015, Shearn-Bochsler et al. 2019, Duriez et al. 2023, Ringenberg et al. 2024, Wünschmann et al. 2024). For Accipitridae species native to the United States, Gonnerman et al. (2024) identified no experimental infection data, though one limited study on white-tailed sea eagles (*Haliaeetus albicilla*) reported no mortality following infection (Fujimoto et al. 2022). Vultures, which commonly scavenge infected carcasses, likewise remain unstudied in challenge settings despite increased reports of mortality (Ringenberg et al. 2024), particularly black vultures (*Coragyps atratus*), which are highly gregarious with expanding populations in parts of the United States (Zimmerman et al. 2019). Within Falconidae, 2 studies challenged a total of 22 American kestrels (*Falco sparverius*), all of which perished (Hall et al. 2009, Uno et al. 2020). Across raptors and scavenging birds, the limited number of challenge studies resulted in a broad range of potential outcomes, underscoring substantial uncertainty in how these groups respond to infection.

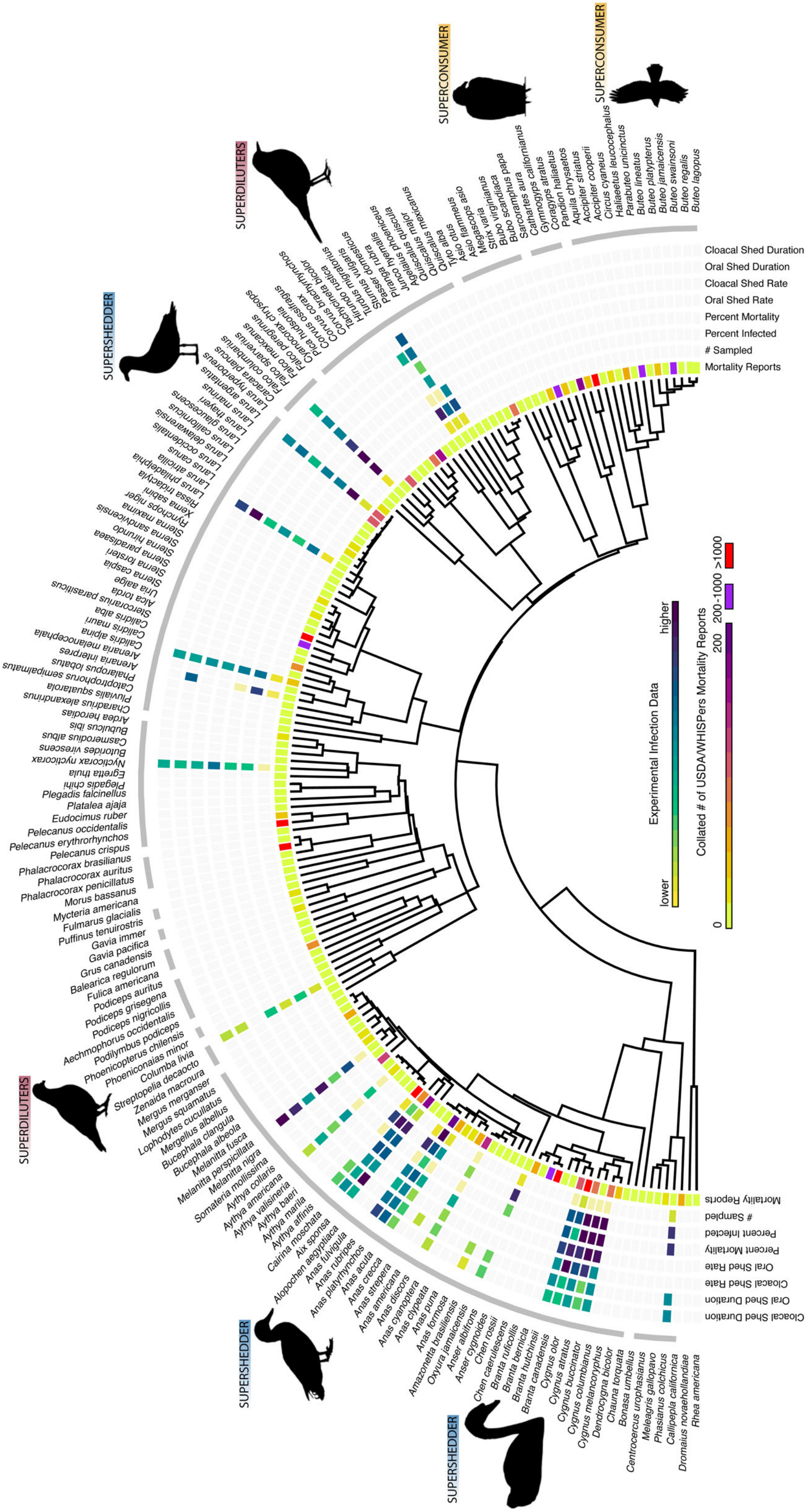

FIGURE 2 (See caption on next page).

Experimental findings can complement field observations and improve interpretation of infection dynamics and potential transmission risks in wild bird populations. However, experimental infection responses must be interpreted within the context of methodological constraints, such as viral dose, route of exposure, prior immune status, and strain-specific effects, and interpreted alongside field-based evidence. Given the logistical, ethical, and biosafety challenges associated with these studies, challenge studies provide valuable but necessarily constrained insights that are not possible to capture in field-based studies. Continued refinement of challenge study designs will support more accurate assessments of response to viral exposure across host species, helping bridge the gap between controlled findings and natural systems. Additionally, maximizing the potential of experimental studies to broaden our understanding of pathogenesis, immune activation, and the cellular pathways underlying divergent host responses is critical. Ultimately, validation of experimental findings through targeted wild sampling is essential to contextualize laboratory results and improve understanding of infection outcomes and transmission processes in natural populations.

Therefore, we explore what can currently be elucidated from the existing literature and highlight critical knowledge gaps. We compiled an updated primer describing host-virus interactions within the HPAIV-wild bird system, emphasizing how seasonal patterns, migratory connectivity, and interspecies interactions contribute to shaping viral transmission dynamics across diverse ecological landscapes. This synthesis draws on recent advances across disparate fields of avian research and places them within the broader context of HPAIV emergence and spread. We evaluated the compiled information describing bird species' life-history strategies, viral responses, and biological traits using qualitative methods, describing host roles across a continuum of host competency and vulnerability. We present this novel framework as the HPAIV host response continuum (Figure 3), which integrates ecological theory with emerging empirical evidence to provide a more nuanced understanding of a host species' role in viral transmission and susceptibility. Finally, we identified critical gaps in the current body of knowledge, which, once addressed, can improve our ability to inform HPAIV surveillance and management strategies while also informing broader avian conservation initiatives.

METHODS

Axis of the HPAIV host response continuum: vulnerability and competency

The response of wild birds to HPAIV H5N1 clade 2.3.4.4b infection, as observed in wild surveillance and challenge studies, spans a continuum across which species can be compared. This variation is shaped by diverse avian life-history strategies and behaviors that influence susceptibility and exposure risk to HPAIV, including colonial nesting, gregariousness, mixed flock foraging, and predatory or scavenger feeding (Harvey et al. 2023, Yin et al. 2023).

FIGURE 2 A phylogram of 167 avian species from the United States in which highly pathogenic avian influenza has been detected during the current outbreak from December 2021 to December 2023, including the 28 species for which experimental data have been collected for at least one disease trait. Colored gradient bars represent the following data: number of mortality reports from the United States Department of Agriculture (USDA) and the Wildlife Health Information Sharing Partnership Event Reporting System (WHISPers; U.S. Geological Survey National Wildlife Health Center 2021, USDA APHIS 2024b) and experimental infection metrics (number [#] sampled, percent infected, percent mortality, oral or cloacal shedding rate and duration), which have been placed at the tips of the branches. Species with a collated USDA and WHISPers mortality count of 200–1,000 are colored purple, while those with counts >1,000 are colored red. Transparent bars indicate where experimental infection metrics are lacking. The phylogenetic tree is a maximum clade credibility (MCC) tree generated from a random sample of 500 trees from the posterior distribution of trees produced by Jetz et al. (2012), which was pruned to the relevant taxa. We plotted data in R using the Phytools package (Revell 2024).

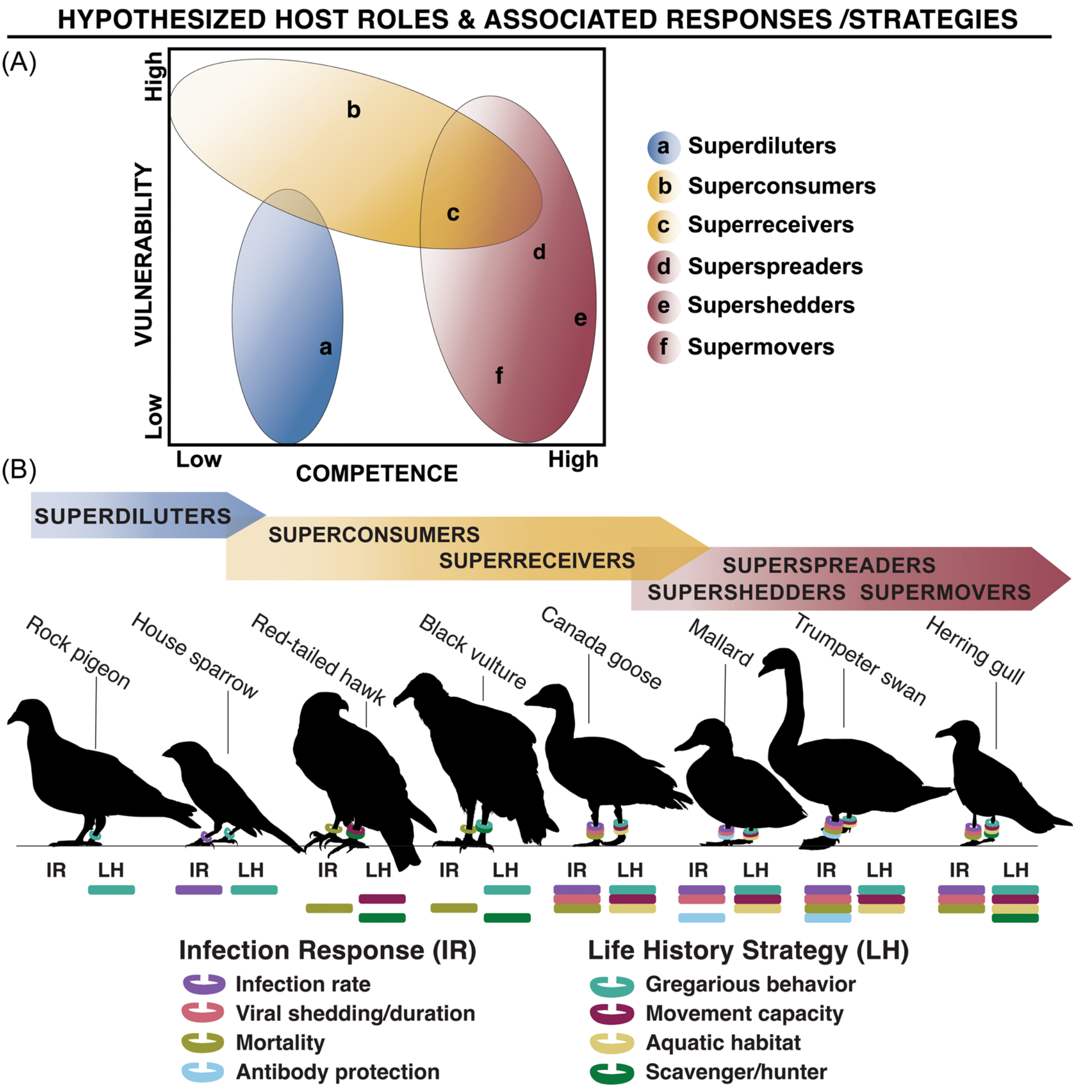

FIGURE 3 The host response continuum for highly pathogenic avian influenza viruses (HPAIV), including hypothesized host roles (A) and associated host strategies (B). Frame A presents a conceptual depiction of the continuum of host responses to HPAIV infection and exposure based on the primary axis of host competence, ability to infect other hosts, and host vulnerability, which integrates susceptibility and exposure risk. Host roles may overlap as they exist on a spectrum, but we highlight distinct host archetypes of interest, such as superdiluters, superconsumers, superreceivers, supershedders, supermovers, and superspreaders (Box 1). In frame B we provide examples of wild bird species as proxies for populations and individuals and their responses based on the spectrum of host responses (in A). We hypothesize that roles are informed by documented infection responses (IR; infection rate, viral shedding or duration, mortality, antibody protection) and associated host life-history (LH) strategy (gregarious behavior, movement capacity, aquatic habitat, scavenger or hunter). A simplified number of host viral responses and strategies are presented and are indicated by leg color bands, with IR shown on the left bands and putatively associated LH strategies on the right bands. Species are not to scale.

The variation in avian life-history strategies and immune phenotypes produces a mosaic of host responses and roles, each shaping viral dynamics. Understanding variation in host responses across infected species may improve our understanding of the complex and dynamic HPAIV system, allowing for differentiation across the broad range of avian host species now affected.

We hypothesized that characterizing host responses along an HPAIV host response continuum (Box 1; Figure 3A), which represents a fluid spectrum of responses informed by the combination of host infection metrics and life-history strategies and traits, would help clarify the diverse roles of wild birds in viral transmission (Figure 3B). We summarize host traits and known disease responses, simplifying many characteristics along a pair of axes to allow for more direct comparisons (see Supplemental 3: Analysis Inputs). Along the *x*-axis, we display host competence (i.e., how effectively they infect other susceptible hosts; Box 1; Martin et al. 2019). Comparatively, along the *y*-axis, we display host vulnerability (Box 1), where placement reflects viral susceptibility and likelihood of exposure. We propose that these axes inform the HPAIV host response continuum, which describes a host's capacity to infect others and a host's likelihood to be infected when exposed to virus.

We examined host responses to exposure and infection across species, recognizing that heterogeneity in responses is expected across individuals (VanderWaal and Ezenwa 2016). Numerous disease systems have demonstrated that a small number of individuals, known as superspreaders, can disproportionately drive pathogen transmission (Lloyd-Smith et al. 2005, Taube et al. 2022). These represent extreme responses by individuals of a host species. However, certain host species may have biological and immunological traits that inform the potential for extreme responses across species (Hawley and Altizer 2011). For example, individuals may vary in host competence and vulnerability, informing their roles as superspreaders, supershedders, and supermovers (Box 1), which respectively have an outsized capacity to infect others, shed virus into the environment, or disperse virus long distances. Superspreaders and supermovers are species with low vulnerability, exhibiting mild or asymptomatic disease, but a high capacity for viral transmission and dispersal, driven by high viral shedding into the environment or contact with other hosts through gregarious behaviors and migratory movements. Mallards (*Anas platyrhynchos*) have been identified as potential supermovers of HPAIV, as infected birds exhibit no changes in body condition or migratory behaviors (Teitelbaum et al. 2023b), or as supershedders of LPAIV by increasing environmental transmission (Arsnoe et al. 2011, Jankowski et al. 2013). Highly vulnerable individuals (i.e., superreceivers; Box 1) are more likely to experience increased contact or exposure via infected individuals or through the environment and may therefore be of higher conservation concern or a potential source of increased local spread. Similarly, superconsumers (Box 1) are highly vulnerable species that prey on infected individuals or scavenge carcasses, exemplified by an increased number of cases in bald eagle (*Haliaeetus leucocephalus*; Nemeth et al. 2023) and other raptor species (Ringenberg et al. 2024). Superdiluter (Box 1) hosts are poor transmitters of HPAIV, exhibiting low viral shedding rates and duration. As a result, they may reduce viable virus pathways within the community and may additionally exclude other susceptible hosts from an area through competition for shared resources or space (Merrill and Johnson 2020). Some commonly peridomestic-associated terrestrial birds, such as house sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*), have been detected with active infections near poultry outbreaks (Ringenberg et al. 2024). These species' host roles are unclear; they have been suggested as potential bridge species in transmitting virus between migratory birds and domestic or backyard farms (Ringenberg et al. 2024). They have documented low shedding levels and minimal disease symptoms, which could result in some dilution due to their seemingly low viral competence and overabundances where they dominate areas and outcompete other species (Caron et al. 2017, Root et al. 2024). However, even superdiluters can play relevant roles as reservoirs in specific ecological contexts or densities, such as by facilitating transmission into poultry farms or when they are in great enough densities (Fuller et al. 2010). As such, species may occupy multiple host roles across the spectrum of responses depending on ecological context and the dynamic nature of host–virus interactions.

We independently defined each axis according to *a priori* hypotheses describing how host traits might influence host HPAIV response phenotypes (Table 1). We then applied these to qualitative modeling frameworks intended to summarize and compare species along the continuum. Using a broad avian conservation framing, we derived hypotheses through a series of discussions among HPAIV system experts and then refined them using available datasets. Given the lack of sufficient data, we do not intend this to be an exhaustive description of HPAIV host responses but rather a demonstration of how these concepts could be applied once more data

TABLE 1 Hypotheses detailing host responses in competent and vulnerable avian species, with associated trait data, data sources, descriptions, and response characterizations. For each axis of the highly pathogenic avian influenza virus (HPAIV) host response continuum—host vulnerability and host competency—we defined *a priori* hypotheses to explore how specific host traits may influence HPAIV phenotypes, contributing to our understanding of host-pathogen dynamics.

Trait	Source[a]	Description	Competent host	Vulnerable host
Wild mortalities	WHISPers/ USDA-APHIS	Number of observed mortalities reported as of 16 Oct 2023	Fewer mortalities in wild observations indicate decreased chance of infection and death (Harvey et al. 2023)	More mortalities in wild observations indicate increased chance of infection and death (Harvey et al. 2023)
Wild subclinical infections	WHISPers/ USDA-APHIS	Number of sub-clinical, hunter harvest, and non-mortality infections, reported as of 16 Oct 2023	Fewer subclinical infections in wild observations indicate decreased chance of infection (Harvey et al. 2023)	
Immunity	Serology- BV-BRC database	Proportion of individuals identified as positive for HPAIV		Lower seropositivity rates indicates a lower instance of antibody protections in wild populations (Caliendo et al. 2022b)
Mortality rate	Challenge studies review	Proportion of individuals who succumbed to infection when challenged with HPAIV H5	Species with lower mortality rates in challenge studies are less likely to die from natural infections (Soda et al. 2022a)	Species with higher mortality rates in challenge studies are more likely to die from natural infections (Soda et al. 2022a)
Infection rate	Challenge studies review	Proportion of individuals who were infected when challenged with HPAIV H5	Species with higher infection rates in challenge studies are more likely to be infected when exposed in wild settings (Soda et al. 2022a)	Species with higher infection rates in challenge studies are more likely to be infected when exposed in wild settings (Soda et al. 2022a)
Viral shedding rate	Challenge studies review	The average maximum $\log_{10}$ 50% egg infectious doses per milliliter (EID) via the oropharyngeal or cloacal route	Greater shedding rates indicate increased capacity to deposit HPAIV in the environment (Gonnerman et al. 2024)	
Viral shedding duration	Challenge studies review	The average number of days that infected individuals shed HPAIV	Longer shedding duration indicates increased capacity to expose other individuals and deposit virus in the environment (Gonnerman et al. 2024)	
Colonial nesting	Birds of the World	Whether an animal nested solitarily, in conspecific colonies, or in mixed-flock colonies	Increased potential for interactions with naive animals, increasing chance of transmission (Ely et al. 2013, Shriner and Root 2020)	Increased potential for interactions with infected animals, increasing exposure risk (Ely et al. 2013, Shriner and Root 2020)

TABLE 1 (Continued)

Trait	Source[a]	Description	Competent host	Vulnerable host
Foraging strategy	Birds of the World	Whether an animal forages alone or in pairs, in conspecific flocks, or in mixed-species flocks.	Increased potential for interactions with naive animals, increasing chance of transmission. (Ely et al. 2013, Shriner and Root 2020)	Increased potential for interactions with infected animals, increasing exposure risk (Ely et al. 2013, Shriner and Root 2020)
Continental range extent	Literature review	Number of continents species' range covers	Increased potential to disperse virus and introduce it to naive populations. (Gass et al. 2023b)	
Lat. range extent	eBird status and trends	The latitudinal distance between the northern- and southernmost points of the annual range	Increased potential to disperse virus and introduce it to naive populations. (Gass et al. 2023b)	
Long. range extent	eBird status and trends	The longitudinal distance between the northern- and southernmost points of the annual range	Increased potential to disperse virus and introduce it to naive populations. (Gass et al. 2023b)	
Migratory status	AVONET	Whether a species is migratory, partially migratory, or resident	Informs potential to transmit locally or disperse virus to naive populations (Gass et al. 2023b)	
Migratory connectivity	Literature review	Mantel correlation coefficient (r_m) or strength of migratory connectivity (MC)	Increased potential to disperse virus across populations and their heterospecifics (Gass et al. 2023b)	

[a] External data sources are publicly available at their respective web interfaces: WHISPers (whispers.usgs.gov), USDA-APHIS (aphis.usda.gov/livestock-poultry-disease/avian/avian-influenza/hpai-detections/wild-birds), BV-BRC (bv-brc.org), challenge studies review (doi.org/10.1098/rspb.2024.1845), Birds of the World (birdsoftheworld.org), eBird status and trends (science.ebird.org/en/status-and-trends), and AVONET (doi.org/10.1111/ele.13898).

become available. Further, hypotheses could reflect both our understanding of the HPAIV system and the relevant management objectives; therefore, hypotheses describing competence and vulnerability may differ by application (e.g., wild bird conservation versus domestic poultry risk) or user preference. Some hypotheses were shared between competence or vulnerability, such as infection rate and gregarious behavior, as animals must first be infected to infect other species.

To better differentiate between the 2 axes, we used mortality as a proxy for vulnerability (see Supplemental 3: Analysis Inputs), reflecting how readily an animal was immunologically susceptible to infection and severe disease (Pacioni et al. 2015). While HPAIV can have many negative impacts on avian hosts (Weber and Stilianakis 2007, Ramey et al. 2022), data on fitness outcomes (e.g., physiological conditions, reproductive output) and disease pathogenesis remain limited across taxa and regions (Martí-Garcia et al. 2025). As a result, we used mortality as an indicator of vulnerability, expecting that species with greater vulnerability would have higher incidence of infection and mortality when exposed to HPAIV, both in challenge studies and in wild detections. We further predicted that vulnerability may be increased by behavioral exposure, such as gregariousness in animals that move, roost, forage, or nest colonially (Shriner and Root 2020).

By contrast, we considered host competence as a continuous trait, reflecting where species fall along the spectrum from low to high ability to transmit HPAIV and infect other hosts, directly (bird to bird) or indirectly through the environment (Gervasi et al. 2015). Successful viral transmission can be summarized into 2 primary compartments: exposure risk and species competence (P. Huang et al. 2023). Species competence indicates a species' ability to effectively transmit virus and infect other hosts (i.e., requiring viral replication and sufficient shedding for forward transmission; Box 1). Within this framework, we defined high-competence hosts as species that support viral replication and shedding sufficient virus to infect other hosts. Accordingly, hosts positioned higher on the competence spectrum would also have a greater capacity to shed virus, as indicated by increased shedding rates (i.e., $\log_{10}$ EID_{50} per mL or equivalent unit) and durations, via the oral or cloacal pathways based on challenge studies (Gonnerman et al. 2024). These traits may be evidenced by a higher incidence of subclinical infections (i.e., hunter harvest, live surveillance, and detections of antibodies) and lower mortality rates in wild birds and challenge studies (Gonnerman et al. 2024). At local scales, we expected gregarious behavior to be an indicator of competence, as animals that forage or nest communally will have more interactions with naive hosts compared to solitary ones. To assess host-mediated viral movement capacity across scales, we also considered annual movement behavior, range extents, and gregarious associations. At broader spatial scales, we expected some high-competence hosts to exhibit more diffuse (i.e., reduced migratory connectivity) and far-reaching migrations (i.e., greater geographical range extents), which have been correlated with increased viral spread (Hill et al. 2022, Roberts et al. 2023, Gass et al. 2023a), potentially due to a greater overlap with naive populations. Conversely, hosts with limited viral replication, low shedding intensity or duration, and restricted contact rates are expected to fall toward the lower end of the competence spectrum.

To develop a more comprehensive understanding of HPAIV dynamics in wild bird species of the United States, we addressed 3 primary aims. First, we provide a primer for the HPAIV system across topics, including viral evolution, pathogenesis, and immunological response in wild birds; seasonality, age, and migratory dynamics in wild birds; and challenge studies in wild bird species. Second, we leveraged the breadth of existing data by combining viral responses (e.g., susceptibility, immunological response, subtype composition) into a qualitative multivariate analysis to examine putative host roles across the HPAIV response continuum (Figure 3) by comparing viral response with underlying biological drivers (i.e., life-history strategy, phylogeny, physiology, functional traits, overlap with poultry production). We explained heterogeneity in disease risk across bird taxa and examined inconsistencies and uncertainties in the roles of life-history traits and biological drivers, given the limited available data. Third, we compared how species' placement within the HPAIV host response continuum may be influenced by current data limitations, to identify gaps in current information and understand how additional information could improve our ability to inform HPAIV management and conservation efforts.

Multivariate modeling of host response

Overview and approach

We compared avian host species according to their placement on the vulnerability and competency axes of the HPAIV host response continuum. Available datasets describing viral response and ecological traits (Harvey et al. 2025) were subject to heterogeneous data types, misaligned data resolutions, missing data, and uneven sampling effort. Additionally, species-specific metrics generated from literature reviews represented information from various sources and methods aggregated into a single measure. Thus, we anticipated a meaningful amount of noise among datasets, which reduced the ability to identify statistically significant relationships. As such, common univariate approaches were insufficient to disentangle numerous interacting elements (Yeater et al. 2015), so we instead applied qualitative multivariate approaches to rank (non-metric multidimensional scaling [NMDS] scores) or group host species (mixture models).

The sub-aims for our modeling were 1) to characterize bird species in the context of the HPAIV host response continuum according to available viral responses, life history, and movement traits; 2) to identify ecological traits associated with competent and vulnerable species; and 3) to measure pairwise overlap between species ranges to assess the potential interactions between vulnerable and competent host species along with the domestic poultry industry (Figure 4). We used 2 methods for characterizing species according to our expectations of competent and vulnerable hosts. First, we used a flexible, user-defined score based on the NMDS ordination method to rank species according to the independent rank-order differences among traits and metrics (Dexter et al. 2018). Second, we used a statistical method, Bayesian nonparametric mixture modeling, to analyze differences in the distributions of individual traits and classify species into several clusters, interpreted considering our *a priori*

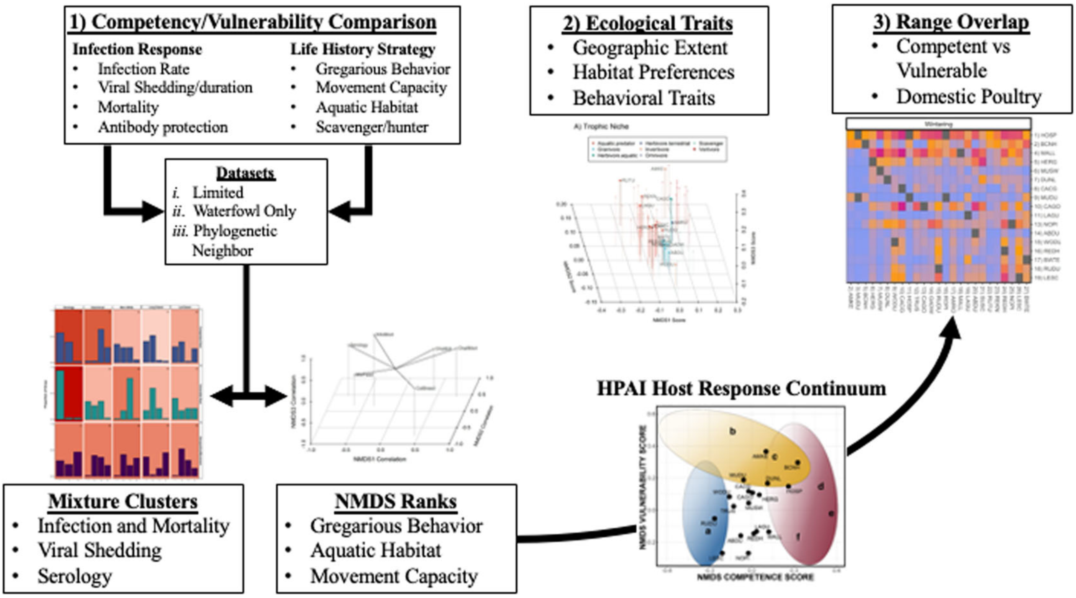

FIGURE 4 Depiction of the modeling framework comparing avian species in the United States according to their placement on the highly pathogenic avian influenza virus (HPAIV) host response continuum. The flow diagram shows how we integrated information describing host infection response, life-history strategies, and broader ecological traits and compared results across mixture models and non-metric multidimensional scaling (NMDS) analyses.

hypotheses (Valle et al. 2022). We chose these methods to compare many traits and metrics simultaneously, and they were generally considered robust to a certain amount of missing data (Kenkel and Orloci 1986, Maleki et al. 2019). The NMDS approach produces scores that can be used to rank species, which may be used by decision-makers with limited resources to prioritize species. However, NMDS is a dimensionality reduction method for data visualization rather than for formal statistical inference, as it provides no associated accuracy or uncertainty estimates. Additionally, NMDS ranks are relatively responsive to available data, requiring thoughtful curation of datasets and formulation of hypotheses *a priori*. Mixture models are useful when observations (e.g., species, individuals) are to be classified into broader groups; however, clusters may be uninformative if many species clump together for certain traits and metrics, or if species are missing informative data inputs. The combination of NMDS rankings and mixture model clustering can enhance interpretation: concordance between methods provides confidence in species' functional groupings along the host response continuum, while discrepancies indicate species for which data may be sparse, heterogeneous, or context dependent, and where inference may be uncertain.

Phylogenetic neighbor and waterfowl-only analysis

Because of inconsistencies in data collection and availability across countries, we focused our analyses on data from the United States (Table 1). While NMDS and mixture model methods can handle missing data to some degree, missing values may still affect outputs and alter inference (Podani 2005). As our reviews demonstrated deficiencies in data describing host response to HPAIV infection (only 27 of 133 species considered had comparable data available), it was likely that rankings would change as more information became available. Thus, we applied our analyses to 3 datasets, including a limited dataset that excluded species with excessive missing values ($n = 27$), a waterfowl-only dataset (Family Anatidae; $n = 14$), and a phylogenetic neighbor dataset ($n = 68$) where we imputed missing data from the nearest phylogenetic neighbor.

Because data availability varies substantially across affected species, we first conducted an analysis using a reduced dataset that included only species with sufficient empirical data to support direct comparisons. The limited dataset comprised 27 species for which key metrics describing host response to infections and transmission were available while minimizing missing values.

Many species may now be contributing to HPAIV dynamics, but waterfowl species (Family Anatidae) play a key role given their distribution, historical role as IAV reservoirs, and our understanding of their current role in viral dispersion (Hénaux and Samuel 2011, Blagodatski et al. 2021, Damodaran et al. 2025). Additionally, waterfowl species are widely studied compared to other avian families. Thus, we subset data to a waterfowl-only dataset to reduce the impact of missing data on ordination without having to resort to data imputation, facilitating interpretation within a group where data are more widely available.

Closely related species tend to share similar viral competence (Huang et al. 2019, Wang et al. 2019). Therefore, we used the nearest phylogenetic neighbors as proxies for species with missing data to infer exposure risk and competence in transmitting HPAIV H5. To determine the nearest phylogenetic neighbor, we created a 95% majority-rule consensus tree by sampling from a distribution of 10,000 trees derived from BirdTree.org using the Hackett backbone (Jetz et al. 2012). We determined the nearest neighbor using the smallest pairwise distance, based on branch lengths, calculated with the function cophenetic in the R package ape (Paradis and Schliep 2019). To avoid assigning unrealistic values from distantly related species, we limited imputation to only use data from species within the same family as the animal with missing data, resulting in the phylogenetic neighbor dataset. We then repeated clustering and ordination methods using the phylogenetic neighbor dataset and compared the results with those from the limited dataset to demonstrate how ranks changed with increased information. We excluded rankings and scores for species where data were imputed, to discourage inference for species for which we have insufficient information to describe viral response. This final approach demonstrated limitations of currently available data by showing the potential for change in inference following future data collection.

Non-metric multidimensional scaling

Non-metric multidimensional scaling is an ordination and data-visualization technique (Kenkel and Orloci 1986) of the same general family as the more widely known principal components analysis (Legendre and Legendre 2012). It is unique in that it does not consider the distance between data points but rather attempts to preserve ranking among them by describing rank-order correlations among traits and metrics (Agarwal et al. 2007). This allows flexibility in handling various data types, such as categorical and non-linear inputs, as well as inputs associated with sampling noise, like those aggregated within our literature review. The ultimate purpose of NMDS is to rank sample units (i.e., species) so that the final scores minimize the dissimilarity between them and the true order of individual traits and metrics.

The NMDS technique requires a distance matrix describing the relative differences in trait values between species (Kenkel and Orloci 1986). Given that our data included both categorical and continuous variables, the Gower distance measure (Gower 1971) was most appropriate (Greenacre and Primicerio 2014). Categorical traits could be input in 2 ways, depending on the understanding of the system. When the relationship between classes was known but not the magnitude or direction, such as with habitat and forage type, traits could be defined using binary dummy variables indicating which categories each species occupies (Lee and Yun 2003). If the differences between classes could be specified relative to one another, categorical data could be considered ordinal, where user-defined distances represented the difference between categorical values (Dexter et al. 2018). For example, we could group hosts according to whether they are fully, partially, or non-migratory, where ordinal increases in the tendency to migrate would be expected to correspond to increases in competency (see Supplemental 2: Migratory Connectivity and HPAI).

We created distance matrices and conducted NMDS analysis using the vegan package (Oksanen et al. 2001) in program R. We subset traits and species similarly for the mixture models. For the limited, waterfowl-only, and phylogenetic neighbor datasets, we removed traits and metrics with no variation across samples and species with >4 missing data points. For the limited and waterfowl-only datasets, we included only species with at least one trait describing shedding response (i.e., cloacal or oropharyngeal shedding or duration; Table S1, available in Supporting Information) when ranking species by host competence. We similarly included only species with infection or mortality rate estimates from challenge studies when ranking species by vulnerability. This was to ensure that at least one viral response trait was available for each species included in the analysis. We assessed NMDS outputs using a permutation-based approach, in which we shuffled the rank orders of the inputs and evaluated them until we could no longer identify a better ranking (Dexter et al. 2018), as defined by a stress metric measuring how well the ordination matches the inputs. Stress values <0.2 indicated an appropriate goodness of fit.

To translate NMDS scores to ranks, we first calculated Spearman's correlation between species-specific scores and inputs and plotted results to visualize relationships. For example, if an NMDS score was positively correlated with several migration and distribution traits (i.e., migratory connectivity and range, indicating greater capacity for movement), a higher score would indicate a greater ability to spread HPAIV according to our *a priori* hypothesis (Table 1). As scores could be ranked and interpreted in the context of any combination of hypotheses, and different axes may have different relationships with inputs, we sought a single metric that incorporated expectations of how traits and metrics influence HPAIV dynamics into a final set of rankings. To do this, we summed the product of NMDS scores with their trait correlations and a user-defined weight representing *a priori* hypotheses, such that

$$S_{spp} = \sum_1^N \sum_1^M (s_{n,spp} \rho_{n,m} \omega_m)$$

where n indicated an NMDS axes from 1 to N, m indicated one of M input traits or metrics, spp specified a species of interest, ρ represented the correlation between scores along axis n and input values for trait m, ω was a user-defined value representing *a priori* hypotheses describing the expected direction of the relationship to trait m, s was the individual axis score, and S was the final score used for ranking species. We specify ω as +1 or −1 to represent the directional influence of a trait or metric on a species rank, but other values could be supplied to represent relative differences in influence among traits or metrics (i.e., a ω of 0.5 would be less influential than a ω of 1). Additionally, if particular traits or metrics were considered relevant to grouping species but not included in the final ranking used for decision-making, these inputs could instead be supplied to the NMDS with a weight of 0 to limit their influence on ranks. However, adjusting weights had only minor impacts on rankings compared to which input and species were included in the analysis. We sorted the final adjusted scores (S_k) in descending order to produce a ranking, with higher values indicating greater association with hypothesized traits or metrics.

Ecological niche NMDS

While vulnerability and host competence greatly influenced which species were most relevant for conservation, we must also consider how species overlap in ecological space to identify likely transmission points within communities. To do this, we visualized the relative overlap in ecological space among species across a set of categorical descriptors using NMDS. We conducted this analysis independent of comparisons of competency and vulnerability, as we wished to focus on shared overlap. Whereas the previous NMDS compared ordinal traits as inputs to rank species, here we instead supplied binary data indicating ecological traits to identify the degree of overlap in ecological space (Jackson et al. 2012). From the AVONET database (Tobias et al. 2022), we extracted trophic niche (e.g., aquatic herbivore, omnivore, scavenger), habitat type (e.g., coastal, forest, grassland, wetland), habitat density (dense, semi-open, or open), and migratory status (i.e., fully-, partially-, or non-migratory), all specified as binary dummy variables. From our review of the migratory literature, we recorded regional migratory destinations (i.e., Palearctic, Neotropical, Afrotropical) as binary dummy variables where one indicated an animal migrated to a given region from North America (Nearctic). We used behavioral descriptors from Birds of the World (Billerman et al. 2022) as ordinal inputs defining species as gregarious, colonial breeders, and mixed-flock foragers. We used NMDS to score individual species, then plotted the results to visualize potential co-occurrence among species.

Animal range overlap

We assessed the potential for competent hosts to interact with vulnerable species by comparing overlap in annual and seasonal ranges. We used eBird status and trends range estimates (Fink et al. 2022) to describe the distribution of each species, where data were available, and calculated pairwise species range overlap for species in our limited dataset. We used NMDS rankings from our limited dataset to define competency and vulnerability of a species. We calculated percent overlap for each species pair using the st_intersection and st_area functions from the sf package (Pebesma and Bivand 2023) in the R computational environment.

Beyond wild populations interacting, the spread of HPAIV between wild birds and commercial poultry operations was also a known nexus of spillover, where wild populations could both introduce virus to commercial farms or potentially be infected should they be in the vicinity of a poultry outbreak (Prosser et al. 2024). Locations of individual poultry operations were not available within the United States, so we used modeled poultry farm locations, produced from a combination of probabilistic modeling and processing of aerial imagery (Patyk et al. 2020), as inputs to describe the distribution of poultry farms within the conterminous United States.

As these poultry farm locations are estimated with uncertainty, we further summarized individual farm locations using 50%, 25%, and 10% kernel density estimates (KDE) to better characterize the poultry distribution. We then estimated the area overlap (km^2) between the seasonal and annual ranges of vulnerable and competent host species and each KDE for poultry operations.

Bayesian non-parametric mixture model

Given the degree of uncertainty and noise in the available datasets, we applied a second modeling framework that grouped animals by relevant traits, which could then be interpreted in the context of the HPAIV continuum. By grouping instead of ranking hosts, we de-emphasize potential spurious differences among data inputs related to insufficient data availability to instead favor broader similarities in traits associated with vulnerability and competency. To discern how species grouped together based on available trait data, we used a Bayesian non-parametric mixture model (Valle et al. 2022), which estimates the most likely clustering of a group according to a supplied dataset. This model assumed that each species belongs to one of several clusters, based on a probability distribution. The probability of belonging to cluster k, out of a maximum of K clusters, was defined by vector $\boldsymbol{\theta}$ (Valle et al. 2022). Additionally, each cluster k was characterized by a discrete categorical distribution of input variables $\boldsymbol{\Phi}$, representing how clusters were distinguished from one another (Valle et al. 2022). Unlike commonly used clustering methods (such as k-means, hierarchical clustering, or Gaussian mixture models), this model is less restricted by missing data among input variables. Bayesian non-parametric mixture modeling is well-suited to estimating clusters of species with similar traits and metrics that contain discrete and continuous variables, as well as missing data.

This model used a categorical distribution, so trait values were discretized into bins. If not already discrete, data were binned by dividing the range of observed values into 5 evenly spaced bins. We clustered species into groups using the bayesmove package (Valle et al. 2022) in program R (version 4.4.2; R Core Team 2023). For models to run, there must be adequate variation among the set of traits and metrics supplied. To ensure enough variation to allow model convergence, we subset data to only include traits and metrics with at least 2 bins containing at least one species, and species could only have at most 4 missing data points. We performed this subsetting for each dataset: the limited, waterfowl-only, and phylogenetic neighbor datasets. We ran models using 100,000 Markov chain Monte Carlo (MCMC) iterations with the first 50,000 treated as the burn-in and determined convergence visually via trace plots. We repeated model runs 3 times to ensure they consistently converged on the same posterior distributions. We set the maximum number of clusters to 5 for the limited and phylogenetic neighbor datasets and 3 for the waterfowl-only dataset (because of the limited number of species) and assigned hyperparameter prior specification as described in Valle et al. (2022). We determined the likely number of clusters by evaluating the fewest number of clusters representing ≥90% of all group assignments and a visual assessment to determine if cluster-specific distributions of traits and metrics were biologically relevant (Cullen et al. 2022). Additionally, we assigned species to clusters when ≥50% of samples from the posterior distribution were attributed to a single group. Species that did not reach the ≥50% threshold were unclassified because of uncertainty in cluster assignment.

To compare resulting clusters identified from mixture models in the context of vulnerable species and competent hosts, we compared clusters with each trait separately. We ranked clusters according to their average bin value for each trait. To summarize clusters, we described clusters according to which traits and metrics were highest ranked or whose average was within 0.25 units of the highest rank, to avoid ignoring similarly scored groups. This threshold value was subjective and did not affect the model outlets, only our qualitative interpretation of the clusters. A larger threshold value could be used to be more inclusive, or smaller to be more restrictive of what is considered the top-ranked cluster. We interpreted clusters in the context of *a priori* hypotheses for vulnerability and host competence (Table 1).

RESULTS

NMDS results

Competent host

The NMDS scores describing host competency using the limited dataset (Figure S1, available in Supporting Information) showed a strong correlation with migratory connectivity (axes 1 and 2), AVONET migratory status (axis 2), mortality and infection rates observed in challenge studies (axis 1), colonial breeding status (axis 3), and the annual count of subclinical infections observed in monitoring databases (axis 3). After ranking species by NMDS scores (Figure 5), we identified house sparrow (rank score = 0.401) as the most competent host species, followed by black-crowned night heron (0.379), American kestrel (0.293), mallard (0.231), and herring gull (0.190). The lowest ranked species included lesser scaup (−0.411; *Aythya affinis*), ruddy duck (−0.399; *Oxyura jamaicensis*), and blue-winged teal (−0.294; *Spatula discors*). Using the phylogenetic neighbor data, we found that American kestrel became the top-ranked species for host competence (rank score = 0.459). When only considering species represented in both limited and phylogenetic neighbor datasets, mute swan (0.439; *Cygnus olor*), trumpeter swan (0.397; *Cygnus buccinator*), herring gull (0.273), and Canada goose (0.239; *Branta canadensis*) were the next most highly ranked species. The least competent hosts according to this dataset were blue-winged teal (−0.526), ruddy duck (−0.482), and redhead (−0.387; *Aythya americana*). When considering the waterfowl-only dataset, mallards were the most highly ranked for host competence (rank score = 0.545), followed by mute swan (0.333), trumpeter swan (0.244), and Canada goose (0.220).

Vulnerable species

The NMDS scores describing which data factors best inform our *a priori* hypothesis for describing host vulnerability to HPAIV using the limited dataset (Figure S2, available in Supporting Information) showed strong correlation with infection (axis 2), mortality rates (axis 1) observed in challenge studies, colonial breeding status (axis 2), seropositivity rates (axis 1), and wild mortality (axis 1). After ranking species by NMDS scores (Figure 6), we identified black-headed gull (rank score = 0.499) as the most vulnerable host species, followed by American kestrel (0.492), Muscovy duck (0.247; *Carina moschata*), ring-necked pheasant (0.234; *Phasianus colchicus*), and black-crowned night heron (0.223). The lowest ranked species for vulnerability included blue-winged teal (−0.458), lesser scaup (−0.358), northern pintail (−0.331; *Anas acuta*), and redhead (−0.305).

Using the phylogenetic neighbor dataset, we found that black-headed gulls remained the highest ranked for host vulnerability (rank score = 0.639) when considering only species found in the limited dataset (Figure 6). Other species ranked highly for vulnerability included herring gull (0.377), trumpeter swan (0.284), and mute swan (0.276). Lowest ranked species for vulnerability included redhead (−0.763), blue-winged teal (−0.729), red knot (−0.649; *Calidris canutus*), and northern pintail (−0.570). When considering the waterfowl-only data, trumpeter swans were the most highly ranked for host vulnerability (rank score = 0.631), followed by mute swan (0.562), wood duck (0.407; *Aix sponsa*), and Muscovy duck (0.198). The lowest ranked species for vulnerability included the blue-winged teal (−0.589) and ruddy duck (−0.396).

Two-dimensional plots of NMDS scores

When comparing 2-dimensional plots of NMDS scores for vulnerability and competency for the limited dataset (Figure 7), most species clustered centrally, indicating they may have a lower potential to exhibit extreme host responses.

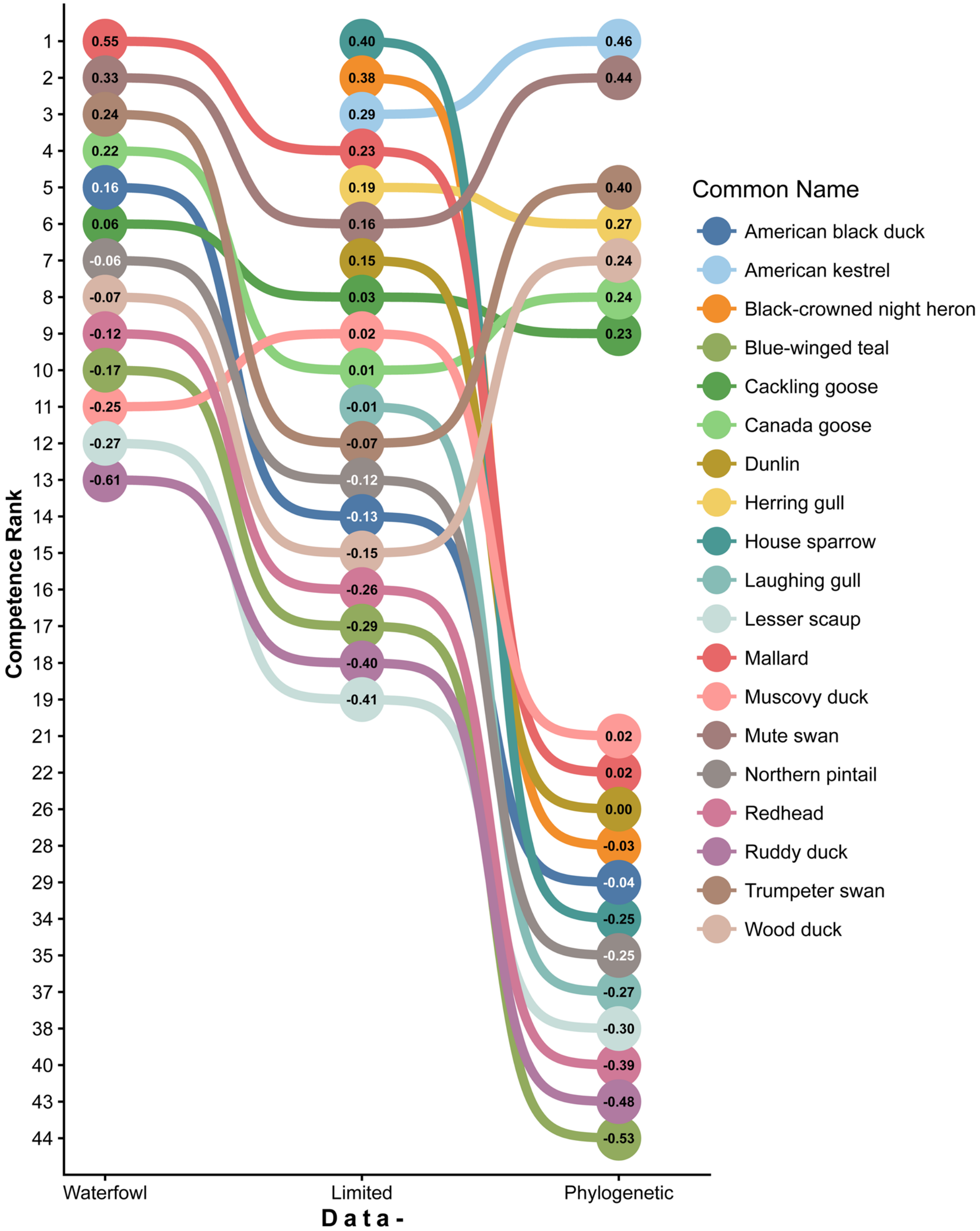

FIGURE 5 Bump chart showing relative host competence rankings to highly pathogenic avian influenza viruses (HPAIV) for avian species in the United States based on data collected from multiple sources. Wild infection data collected from December 2021– January 2024. Species are ranked across 3 datasets: waterfowl-only, limited, and phylogenetic neighbor. Lines connect each species' rank across datasets to illustrate changes in ranking. Breaks in lines indicate species excluded from one or more datasets because of missing values. Points show species-specific ranks, with the non-metric multidimensional scaling (NMDS) score within each point.

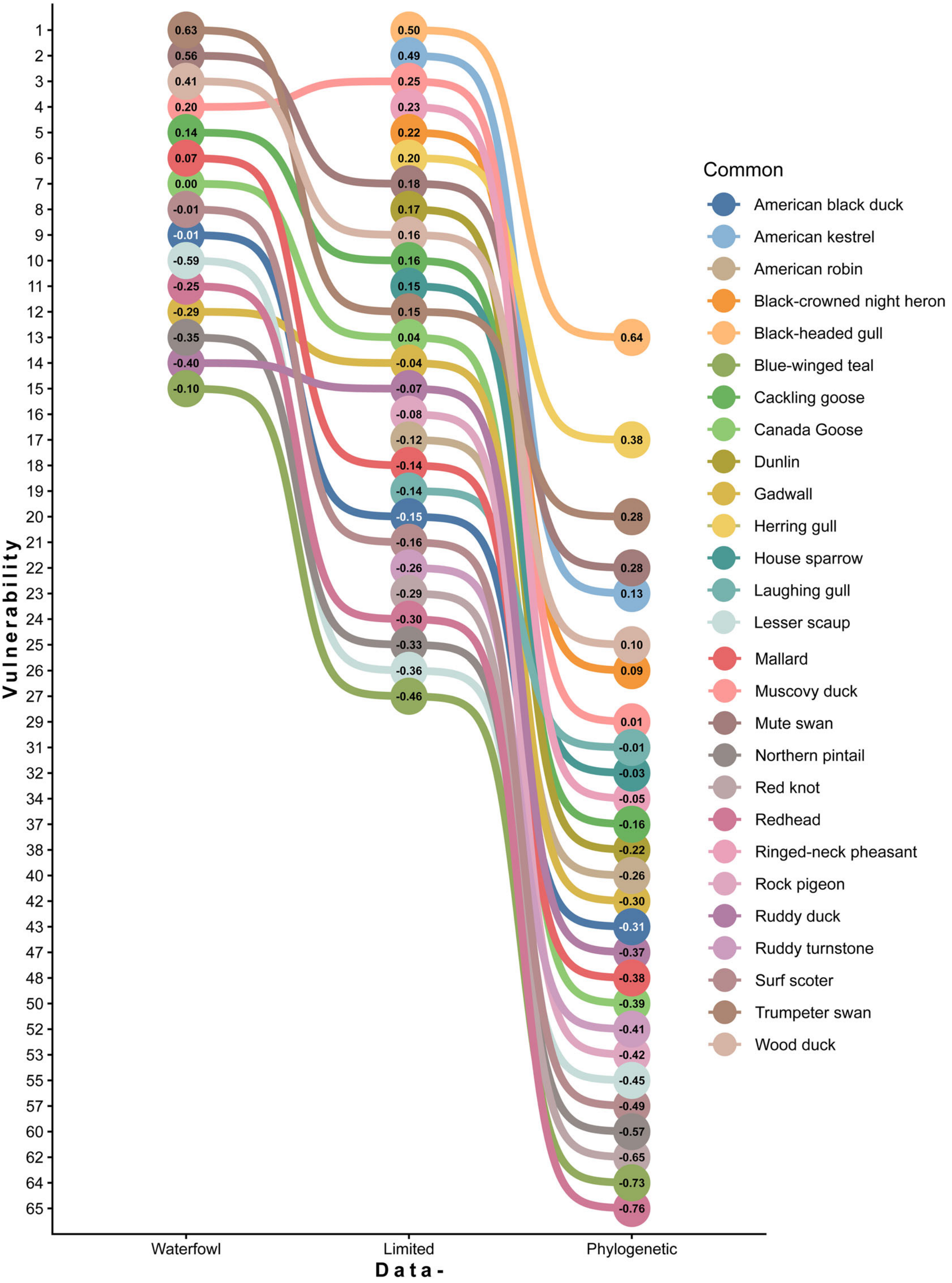

FIGURE 6 (See caption on next page).

However, mallard, laughing gull, and redhead were identified as low vulnerability and slightly above average competence, suggesting these species may be important in transmitting HPAIV. American kestrel, black-crowned night heron, and house sparrow exhibited high axis scores for both vulnerability and competence, suggesting that their potential for high transmission may be limited by their high susceptibility to viral infections. Comparatively, the waterfowl-only dataset demonstrated 2 clusters of trumpeter swan, mute swan, Canada goose, and mallard as high competence and moderately high vulnerability, demonstrating potential as supermover or superspreader hosts (i.e., hosts with potential for extreme host responses). Cackling goose (*Branta hutchinsii*), American black duck (*Anas rubripes*), northern pintail, blue-winged teal, and lesser scaup scored as moderate competence and low vulnerability, suggesting these species may not demonstrate extreme host responses. The phylogenetic neighbor analysis identified laughing gull, wood duck, and house sparrow as high vulnerability and average competence species, suggesting potential as superreceiver hosts. Cackling goose, dunlin (*Calidris alpina*), and mallard represented high competence and slightly vulnerable species, and American black duck, black-crowned night heron, lesser scaup, northern pintail, and redhead were identified as above average competence and moderate to low vulnerability.

Change in NMDS rankings

We observed multiple shifts in priority when comparing host rankings (Figures 5, 6) in the limited dataset to how they were comparatively ranked in the phylogenetic neighbor dataset. For example, relative to species in the limited dataset, house sparrow showed the greatest change in host competency (−12 ranks), followed by wood duck (+10), black-crowned night heron (−9), trumpeter swan (+9), and mallard (−5). Comparatively, ruddy duck did not shift in its relative placement, whereas 5 species shifted one place: herring gull (+1), cackling goose (+1), Muscovy duck (+1), northern pintail (−1), and redhead (−1). When comparing relative placement of vulnerable hosts, laughing gull showed the greatest change in rank (+10), followed by trumpeter swan (+9), ring-necked pheasant (−7), and Canada goose (−6). Black-headed gull and mallard did not shift in relative ranking for vulnerability, whereas 4 species shifted one place: house sparrow (+1), gadwall (*Mareca strepera*; −1), northern pintail (+1), and blue-winged teal (+1).

Ecological niche NMDS

When we converted NMDS axis scores describing ecological niche to points in 3-dimensional space (Figure 8), the average distance between species was 0.199 units. When comparing distance between the top 5 ranked vulnerable and competent host species, herring gulls and black-headed gulls were the most closely grouped (0.060), followed by herring gull and black-crowned night heron (0.066), black-crowned night herons and black-headed gull (0.085), and house sparrow and ringed-neck pheasant (0.107).

Of all species considered in the limited dataset NMDS rankings, we observed 14 pairings with perfect niche overlap. Of these pairings, trumpeter swan was the most vulnerable species and overlapped with blue-winged teal, northern pintail, and redhead. Comparatively, mallards were the highest ranked competent host represented but only overlapped with American black duck.

FIGURE 6 Bump chart showing relative host vulnerability rankings to highly pathogenic avian influenza viruses (HPAIV) for avian species in the United States based on data collected from multiple sources. Wild infection data collected from December 2021– January 2024. Species are ranked across 3 datasets: waterfowl-only, limited, and phylogenetic neighbor. Lines connect each species' rank across datasets to illustrate changes in ranking. Breaks in lines indicate species excluded from one or more datasets because of missing values. Points show species-specific ranks, with the non-metric multidimensional scaling (NMDS) score within each point.

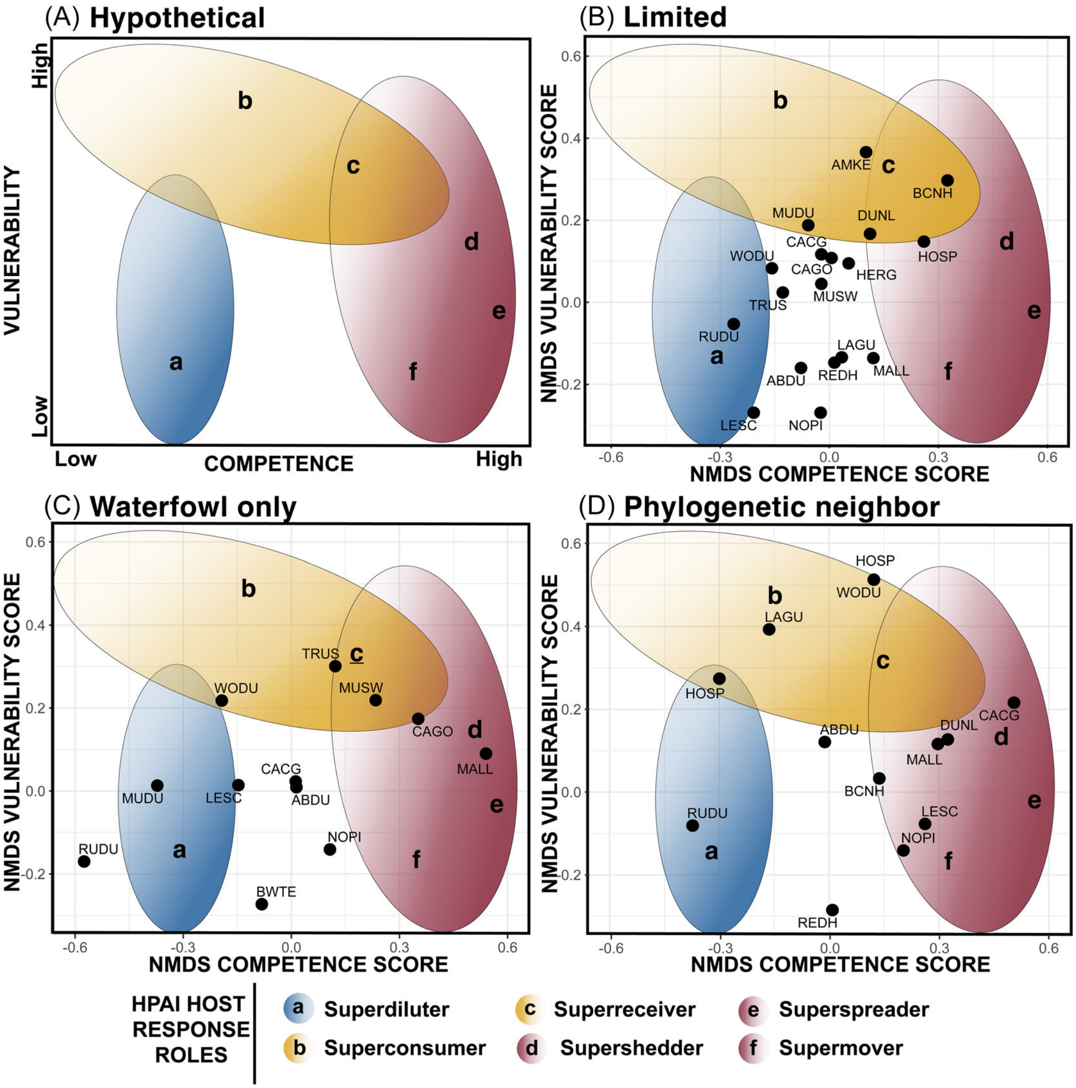

FIGURE 7 Comparison of A) a hypothetical highly pathogenic avian influenza virus (HPAIV) host response continuum and plots of individual host vulnerability and competence non-metric multidimensional scaling (NMDS) scores for the B) limited, C) waterfowl-only, and D) phylogenetic neighbor datasets based on data collected from multiple sources for avian species in the United States. Wild infection data collected from December 2021– January 2024. We also indicate the location of putative host roles on the continuum (a-f). Points are labeled using species alpha bird codes: wood duck (WODU), northern pintail (NOPI), mallard (MALL), American black duck (ABDU), lesser scaup (LESC), redhead (REDH), Canada goose (CAGO), cackling goose (CACG), Muscovy duck (MUDU), trumpeter swan (TRUS), mute swan (MUSW), ruddy duck (RUDU), blue-winged teal (BWTE), herring gull (HERG), laughing gull (LAGU), dunlin (DUNL), American kestrel (AMKE), house sparrow (HOSP), and black-crowned night heron (BCNH).

Animal range overlap

When comparing ranges for vulnerable and competent host species, overlap varied by species pairing and season of the year (Figure 9). Mallards showed the greatest proportion of overlap with other species throughout the year, averaging 65% of a vulnerable species range, although we estimated a higher average for house sparrows during the wintering season (71%). For the 10 most vulnerable species with range data, at least one of the highest ranked

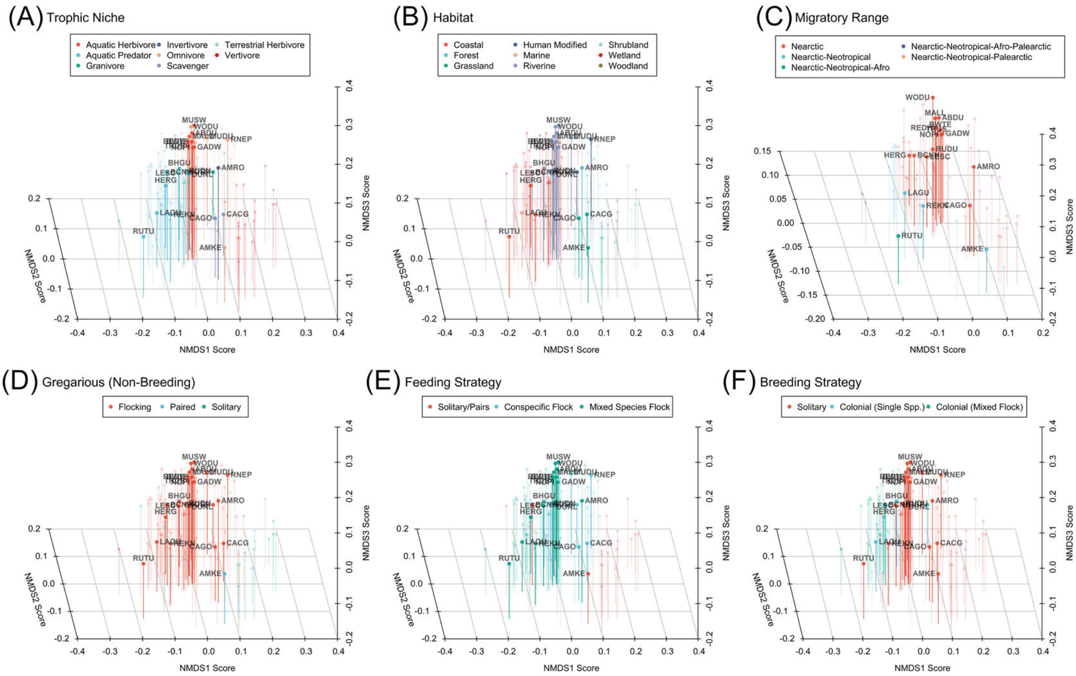

FIGURE 8 Non-metric multidimensional scaling (NMDS) scores describing the ecological niche of bird species in the United States. Scores are plotted in 3-dimensional space and color indicates traits used to produce scores, such as trophic niche (A), habitat association (B), migratory range (C), whether an animal exhibits gregarious behavior (D), the dominant feeding strategy employed by the species (E), and the dominant breeding strategy employed by the species (F). Species plotted closer in space are considered more similar in host traits than those farther apart. Points are labeled using species alpha bird codes: wood duck (WODU), northern pintail (NOPI), mallard (MALL), American black duck (ABDU), lesser scaup (LESC), redhead (REDH), Canada goose (CAGO), cackling goose (CACG), Muscovy duck (MUDU), trumpeter swan (TRUS), mute swan (MUSW), ruddy duck (RUDU), blue-winged teal (BWTE), herring gull (HERG), laughing gull (LAGU), dunlin (DUNL), American kestrel (AMKE), house sparrow (HOSP), black-crowned night heron (BCNH), ruddy turnstone (RUTU), Carolina wren (REKN), American robin (AMRO), house sparrow (HOSP), black-headed gull (BHGU), gadwall (GADW), and ring-necked pheasant (RNEP).

species for host competence (i.e., black-crowned night heron, house sparrow, mallard, or herring gull) was identified as sharing the greatest amount of range overlap with each vulnerable species during at least one part of the year. American robin (*Turdus migratorius*) shared the greatest amount of range overlap with the most densely located poultry operations, followed by wood duck, Canada goose, American kestrel, and mallard (Table 2).

Mixture results

Limited dataset

We used mixture models to group species in the limited dataset according to movement and HPAIV infection metrics, identifying multiple clusters relevant to our *a priori* hypothesis (Figure 1; Table 1). While models were specified to identify 5 clusters, we only identified 4 relevant species clusters, with one cluster being limited to a single species (laughing gull). Cluster one represented a high vulnerability grouping characterized by low antibody prevalence, moderately high wild mortality, high challenge study infection, and mortality, while exhibiting only moderately high shedding rates (Figure 10; Table 3). Cluster 2 included birds with increased host competence,

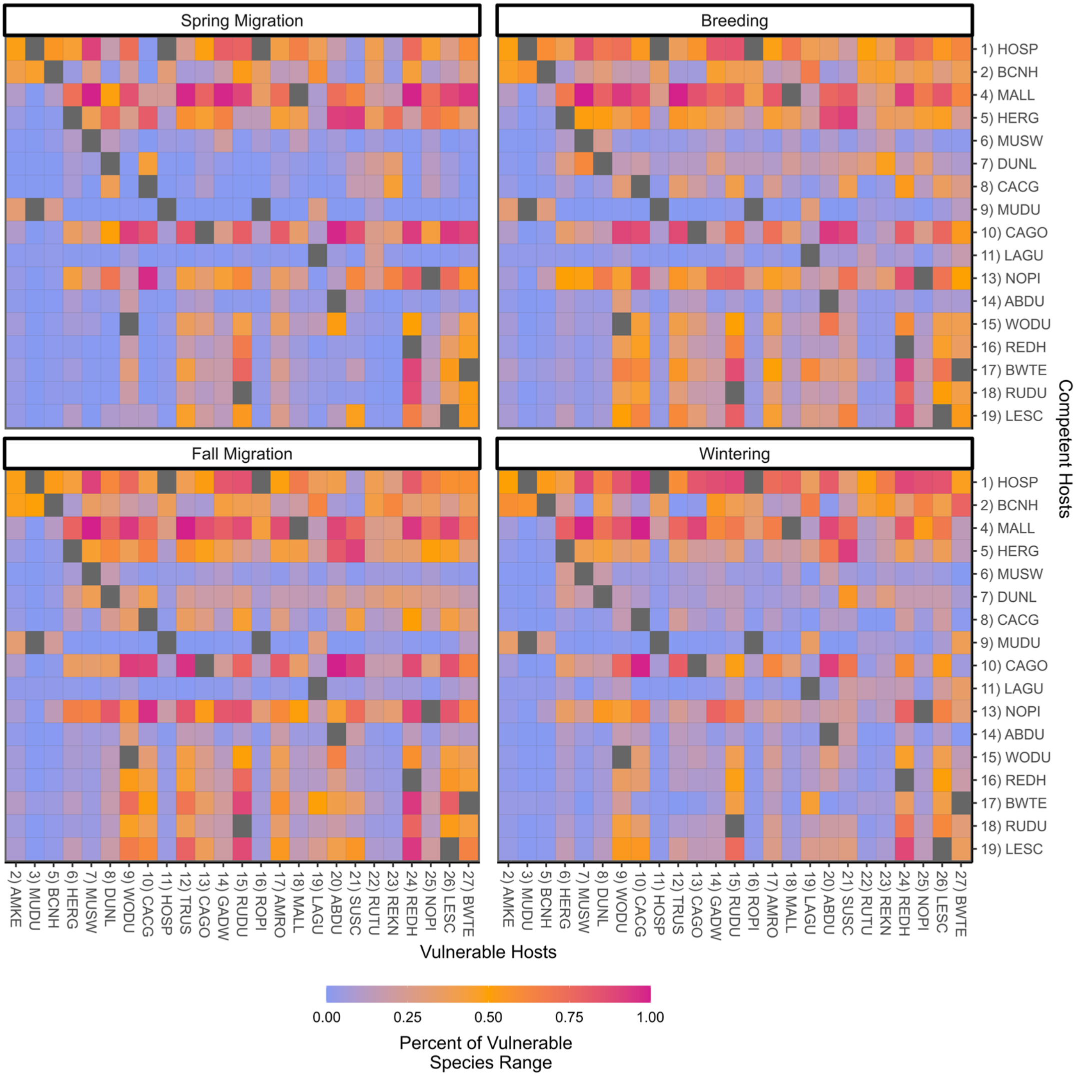

FIGURE 9 Assessment of range overlap between avian species considered vulnerable to highly pathogenic avian influenza viruses (HPAIV) and competent hosts for HPAIV as determined by non-metric multidimensional scaling (NMDS). Overlap is presented as the proportion of the vulnerable species range that is overlapped by the competent host. We present overlap by season, broken into spring migration, breeding, fall migration, and wintering. Species are labeled with associated NMDS rank. Grey indicates no value provided, either because there was no overlap between the 2 species being compared or because the cell corresponds to a single species. Columns and rows are labeled using species alpha bird codes: wood duck (WODU), northern pintail (NOPI), mallard (MALL), American black duck (ABDU), lesser scaup (LESC), redhead (REDH), Canada goose (CAGO), cackling goose (CACG), Muscovy duck (MUDU), trumpeter swan (TRUS), mute swan (MUSW), ruddy duck (RUDU), blue-winged teal (BWTE), herring gull (HERG), laughing gull (LAGU), dunlin (DUNL), American kestrel (AMKE), house sparrow (HOSP), black-crowned night heron (BCNH), ruddy turnstone (RUTU), Carolina wren (REKN), American robin (AMRO), house sparrow (HOSP), black-headed gull (BHGU), gadwall (GADW), and surf scoter (SUSC).

where relevant traits and metrics for cluster formation included a greater number of subclinical observations in the wild, along with greater infection and moderate shedding rates observed in challenge studies (Figure 10; Table 3). We also identified a cluster of low vulnerability hosts in cluster 3, which exhibited longer shedding duration, greater movement capacity, and low mortality in the wild and challenge studies. Cluster 4 included a single species with

TABLE 2 Overlap of annual range for various bird species and kernel density estimates (KDE; km^2) for poultry farms based on modeled location information of birds in the United States (see Patyk et al. 2020). Poultry density was quantified for the 10%, 25%, and 50% most densely populated poultry locations. Total area overlap is presented with non-metric multidimensional scaling (NMDS) ranks (competent and vulnerable) and mixture clusters (cluster), as determined by comparisons of highly pathogenic avian influenza (HPAIV) host response traits. Higher competency and vulnerability are indicated by lower ranks (more positive scores).

Common	Competent	Vulnerable	Cluster	10% KDE	25% KDE	50% KDE
American robin		17 (−0.118)		1,317,686	3,214,297	6,088,922
Wood duck	15 (−0.153)	9 (0.163)	High vulnerability	1,259,178	2,939,247	4,300,871
Canada goose	10 (0.011)	13 (0.037)	High competence	1,204,088	2,777,651	4,688,368
American kestrel	3 (0.293)	2 (0.492)	High vulnerability	1,173,991	2,829,458	5,564,195
Mallard	4 (0.231)	18 (−0.137)	High competence	931,269	2,178,808	4,270,247
House sparrow	1 (0.401)	11 (0.149)	Low competence, low vulnerability	660,438	1,445,457	2,218,002
Blue-winged teal	17 (−0.294)	27 (−0.458)	Low vulnerability	487,425	1,426,360	2,939,908
Rock pigeon		16 (−0.079)		401,487	912,061	1,511,111
Gadwall		14 (−0.041)		365,377	1,106,562	2,480,551
Northern pintail	13 (−0.121)	25 (−0.331)	Low vulnerability	252,117	865,454	2,142,203
Redhead	16 (−0.264)	24 (−0.305)		211,657	617,759	1,703,898
American black duck	14 (−0.133)	20 (−0.152)	High competence	191,200	400,034	547,907
Lesser scaup	19 (−0.411)	26 (−0.358)		181,698	655,885	1,643,589
Trumpeter swan	12 (−0.069)	12 (0.149)	High vulnerability	153,695	578,340	1,194,292
Cackling goose	8 (0.025)	10 (0.159)	High vulnerability	146,573	609,088	1,288,449
Dunlin	7 (0.151)	8 (0.174)		130,031	486,877	936,329
Ruddy duck	18 (−0.399)	15 (−0.071)	Low vulnerability	114,112	449,508	1,412,280
Herring gull	5 (0.19)	6 (0.199)	High vulnerability	99,377	323,093	604,438
Black-crowned night heron	2 (0.379)	5 (0.223)	Low competence, low vulnerability	62,965	325,786	987,672
Mute swan	6 (0.157)	7 (0.176)	High vulnerability	57,405	109,267	138,091
Laughing gull	11 (−0.014)	19 (−0.137)	High competence, low vulnerability	29,533	132,618	278,055
Ruddy turnstone		22 (−0.262)		26,346	182,834	416,675
Surf scoter		21 (−0.162)	High competence	10,920	79,981	170,603
Red knot		23 (−0.29)		4,007	43,025	138,659
Black-headed gull		1 (0.499)		174	812	1,026
Muscovy duck	9 (0.023)	3 (0.247)	High vulnerability	0	3,494	9,958

high shedding rates and movement capacity. Lastly, cluster 5 represented 2 non-traditional HPAIV species, black-crowned night herons and house sparrows, which both have low antibody prevalence rates, low mortality in the wild and in challenge studies, and low to moderate infection rates, suggesting potential to act as superdiluters because of their low transmission capacity.

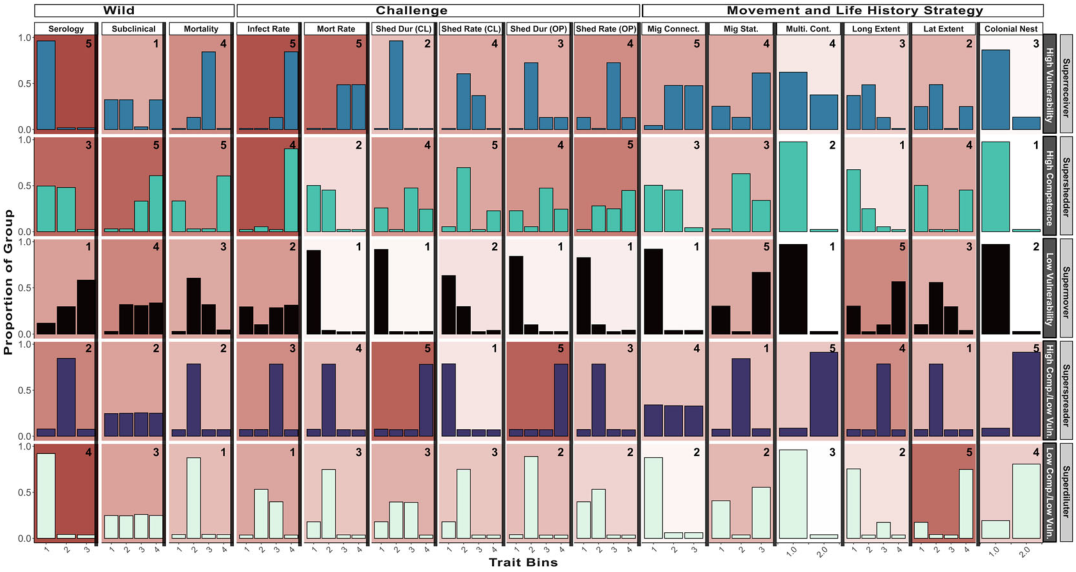

FIGURE 10 Cluster-dependent distributions of traits (rows: responses, wild and challenge, along with bird movement and life-history strategy) from the limited dataset, describing avian species with sufficient infection data available for the contiguous United States during December 2021– January 2024, as estimated by the Bayesian non-parametric mixture model comparing highly pathogenic avian influenza virus (HPAIV) disease response. Background colors indicate weighted average of bin values for a given cluster, and relative ranking among clusters is provided in the top right corner for that trait, where larger rank values and darker red backgrounds indicate greater vulnerability or host competence (except for mortalities, where competency is expected to have a negative relationship). Alignment along the host response continuum (dark grey) and putative host response (light grey) designations are provided to the right of each cluster as determined by association of relevant traits informing the groupings and likely host role across the HPAIV host response continuum.

Waterfowl-only dataset

We identified 3 relevant clusters for the waterfowl-only dataset (Table 3; Figure S3, available in Supporting Information). Clusters one (high competence) and 2 (low vulnerability) were both characterized by higher viral shedding rates. However, cluster one exhibited low to moderate mortality rates and higher instances of subclinical infections in wild observations. Cluster 3 described animals with high movement potential and both above average seropositivity rates and wild mortality reports, but low shedding rates. Therefore, we characterized cluster 3 as superdiluters but note that they may have potential to be supermovers. Comparing waterfowl-only clusters to the limited dataset clusters, American black duck (*Anas rubripes*), mallard, and surf scoter (*Melanitta perspicillata*) all remained high competence hosts, whereas Canada goose shifted to a vulnerable species.

Phylogenetic neighbor dataset

Using the phylogenetic neighbor dataset, we observed uneven reassortment among species priority when comparing the limited clusters to the phylogenetic neighbor cluster analysis (Table 3; Figure S4, available in Supporting Information). Clusters describing vulnerable species did not change dramatically between datasets, sharing most relevant traits with all species except dunlin (limited dataset only). However, we did observe considerable changes in the description and clustering of high and moderate competence hosts between datasets. In the phylogenetic neighbor dataset, high competence hosts displayed greater shedding durations and rates, where secondary

TABLE 3 Species clusters describing host competence and vulnerability for highly pathogenic avian influenza viruses (HPAIV), as defined by categorical mixture models for limited, waterfowl-only, and phylogenetic neighbor datasets. For each dataset used to generate clusters, we provide a characterization of alignment within the dimensions of vulnerability and competence axis (as in HPAIV host response continuum), a description of putative host response is provided, traits and metrics most relevant for describing a cluster, and which species were assigned to each cluster. "Wild" refers to "wild bird surveillance dataset"; "Chall" to "challenge study dataset"; "CL" to "cloacal"; "OP" to "oropharyngeal".

Dataset	Cluster	Axes alignment	Putative host response	Relevant traits and metrics	Species
Limited	1	High vulnerability	Superreceiver	Serology, mortality (wild), infection rate (chall), mortality rate (chall), shedding rate (CL), migratory connectivity, migratory status	American kestrel, cackling goose, dunlin, herring gull, Muscovy duck, mute swan, trumpeter swan, wood duck
	2	High competence	Supershedder	Subclinical, mortality (wild), infection rate (chall), shedding rate (CL), shedding rate (OP), migratory status	American black duck, Canada goose, mallard, surf scoter
	3	Low vulnerability	Supermover	Migratory status, longitudinal extent	Blue-winged teal, northern pintail, ruddy duck
	4	High competence, low vulnerability	Superspreader	Shedding duration (CL), shedding duration (OP), multiple continents, longitudinal extent, colonial breeder	Laughing gull
	5	Low competence, low vulnerability	Superdiluter	Serology, migratory status, latitudinal extent, colonial breeder	Black-crowned night heron, house sparrow
Waterfowl-only	1	High competence	Superspreader	Serology, mortality (wild), mortality rate (chall), shedding rate (CL), shedding rate (OP), migratory connectivity	Cackling goose, Muscovy duck, mute swan, trumpeter swan, wood duck
	2	Low vulnerability	Supershedder	Subclinical, shedding duration (CL), shedding rate (CL), shedding duration (OP)	American black duck, mallard, surf scoter
	3	Moderately vulnerable		Mortality (wild), migratory status, longitudinal extent, latitudinal extent	Blue-winged teal, Canada goose, northern pintail, redhead, ruddy duck
Phylogenetic neighbor	1	High competence	Supershedder	Serology, infection rate (chall), shedding duration (CL), shedding duration (OP), shedding rate (OP), migratory status, colonial breeder	Laughing gull, surf scoter

(Continues)

TABLE 3 (Continued)

Dataset	Cluster	Axes alignment	Putative host response	Relevant traits and metrics	Species
	2	Moderate competence	Superspreader	Infection rate (chall), colonial breeder	American black duck, mallard
	3	High vulnerability	Superreceiver	Serology, mortality (wild), infection rate (chall), mortality rate (chall), shedding rate (CL), migratory connectivity, colonial breeder	American kestrel, cackling goose, herring gull, Muscovy duck, mute swan, trumpeter swan, wood duck
	4	Low vulnerability	Supermover	Serology, subclinical, migratory status, multiple continents, latitudinal extent, colonial breeder	Dunlin
	5	Low vulnerability	Superdiluter	Serology, mortality (wild), migratory status, longitudinal extent, colonial breeder	Black-crowned night heron, blue-winged teal, Canada goose, house sparrow, northern pintail, redhead, ruddy duck

competence hosts demonstrated higher infection rates and propensity for colonial nesting. Of the species in the limited dataset that were categorized as high or moderate competence hosts, only Canada goose changed and was instead assigned to the low vulnerability cluster in the phylogenetic neighbor analysis.

DISCUSSION

An evolving perspective of HPAIV in wild birds

In this analysis, we reviewed and synthesized literature relevant to HPAIV host competency and vulnerability to describe wild birds of the United States according to relevant traits and metrics, including infection metrics, species distributions, resource selection, and gregarious behavioral strategies. Our goal was to characterize current viral dynamics in wild bird populations of the United States to better determine wild bird host roles in HPAIV susceptibility and transmission, and to illustrate how these inferences might change as new data become available. Compiling an up-to-date description of this system supports more informed research and management decisions. This is increasingly important as HPAIV H5Nx of clade 2.3.4.4b continues to adapt to new hosts and systems (Burrough et al. 2024) and has increased in infectivity as observed for previous LPAIV and HPAIV strains (Seekings et al. 2023, Spackman et al. 2023) including increased neurological symptoms and infection via the central nervous system across taxa (Martí-Garcia et al. 2025). Our analysis highlights key knowledge gaps that, if addressed, can improve identification of HPAIV host response roles and prioritization of vulnerable hosts for management.

Our data inputs reflect information at the individual and population levels, which is aggregated to species for the analysis. Therefore, we cannot describe variation in data at the individual or population level. If datasets oversample a specific population, or if small sample sizes over-emphasize specific individuals, then results may be biased towards those individuals. This included a limited capacity to account for spatiotemporal variability in sampling across studies and thus has the potential to bias estimates if sampling itself is spatially or temporally biased. Deficiencies in data describing host viral response prevent a complete description of the HPAIV system in the United States. This limitation is reflected in shifts in species rankings of competence and vulnerability in the NMDS analyses, as well as changes in species cluster assignments in the mixture model (Figures 5, 6, and 10; Table 3). The NMDS analyses provided continuous, relative rankings of species along competence and vulnerability gradients, whereas the mixture model assigned species to discrete functional groups. Concordance between these approaches strengthens inference, while divergence highlights species for which data remain sparse or uncertain.

Despite limitations of data availability, several consistent patterns emerge across methods and datasets that align with current understanding of HPAIV dynamics. Multiple species were consistently associated with high host vulnerability, which may warrant higher priority for disease mitigation and surveillance efforts. These included American kestrel, herring gull, Muscovy duck, and mute swan, which grouped around lower seropositive rates and higher infection and mortality rates in challenge studies. Comparatively, mallards were characterized as high competency hosts across analyses, consistent with prior descriptions of HPAIV system dynamics (Keawcharoen et al. 2008). Their broad abundance in freshwater systems (Beatty et al. 2014), flexible migration strategies from short to long distances (Kraus et al. 2011), and moderate to high shedding rates coupled with low mortality rates (DeJesus et al. 2016, Ducatez et al. 2017) align with our *a priori* criteria for host competency (Table 1) and explain their stable rankings across NMDS datasets (Figure 7).

Although evidence supports mallards as a key driver of HPAIV transmission, waterfowl as a group exhibit variability in infection metrics, which indicate complex, family-wide transmission dynamics. Additionally, American black ducks and Canada geese were consistently ranked as highly competent hosts across analyses, both exhibiting moderately high shedding rates and low mortality rates in challenge experiments, which could indicate an important transmission role and potential as a superspreader, supershedder, or supermover. We also identified several waterfowl species as being consistently vulnerable across analyses: Muscovy duck, mute swan, trumpeter swan, and wood duck. Although these species can contribute to environmental spread due to moderate to high shedding rates

(Brown et al. 2008), they also demonstrated higher infection and mortality rates when exposed (Śmietanka et al. 2013), indicating potential for negative population-level outcomes. Comparatively, northern pintail, blue-winged teal, redhead, and lesser scaup were all inconsistently characterized across analyses, indicating these species' host roles are poorly characterized by available data. However, these groupings are specific to H5N1 HPAIV subtypes, and species may be placed differently on the host response continuum when considering other infection metrics or host traits. For example, while largely asymptomatic when infected with H5N1, northern pintails have been associated with outbreaks along the East Asian-Australasian Flyway (Sullivan et al. 2018). In addition, challenge studies showed that H5N8-infected northern pintails can efficiently replicate HPAIV (Kwon et al. 2018), indicating a broader potential relevance as a reservoir to facilitate long-distance dispersal and viral reassortment. In contrast, a recent study on lesser scaup indicates increasing H5 and N1 antibodies since the 2021 incursion (Sullivan et al. 2025b), suggesting that these species survive H5N1 infections.

Gulls have also recently been identified as an additional key player in HPAIV transmission (Hill et al. 2022, Ineson et al. 2022, Rasmussen et al. 2023), with the initial 2021 incursion of HPAIV H5N1 into North America resulting from a migratory gull. Charadriiformes HPAIV H5Nx sequences are highly clustered, indicating that Charadriiformes- and Anseriformes-associated viral strains provide somewhat differentiated patterns of circulation and transmission (Damodaran et al. 2025). Gulls are abundant across urban and rural landscapes and have been found to serve as urban AIV reservoirs (Ineson et al. 2022), increasing the opportunity for human spillover. Thus, gulls and associated species in shared nesting colonies or feeding flocks may be considered higher priority for surveillance efforts and challenge study research. Consistent with this risk, we identified herring gull as a high vulnerability superreceiver in the mixture model, and this species ranked in the top 10 in both NMDS comparisons of vulnerability and competency (Figures 5, 6, and 7). When experimentally challenged, HPAIV was highly virulent and lethal for immunologically naive herring gulls, and prior exposure to LPAIVs only conferred partial protection (Tarasiuk et al. 2022), indicating higher potential for negative outcomes if exposed. Similarly, in our NMDS comparison, black-headed gulls were ranked as the most vulnerable host species, although we did not identify sufficient movement data for consideration in mixture model or NMDS competency comparisons, likely reflecting their recent range expansion into North America beginning in the 1970s (Cumming 1988). Despite being historical reservoirs of LPAIV, this species exhibits high vulnerability to strains of clade 2.3.4.4b, as demonstrated by experimental studies (Tarasiuk et al. 2022) and wild sampling (European Food Safety Authority [EFSA] et al. 2023). Increased mortality has also been observed in this and other gull species in Europe due to a reassortment between Gs/Gd/96 HPAIV H5N1 and a gull-adapted H13 LPAIV that emerged in Europe in 2022, resulting in a novel genotype (H5N1-A/Herring_gull/France/22P015977/2022-like; euBB; Knief et al. 2023, Fusaro et al. 2024). In previous studies, gull infection response metrics were consistent with vulnerable hosts, exhibiting high infection and mortality rates observed in challenge studies (Ramis et al. 2014), low serological protection detected in wild individuals (Ineson et al. 2022), and increased HPAIV mortalities primarily in Europe (Kareinen et al. 2024). Overall Charadriiformes species, including gulls, may serve as important sources of infection to other host groups, including mammals, raptors, and passerines (Damodaran et al. 2025). From an ecological perspective, gulls exhibit many behaviors conducive to HPAIV transmission, especially colonial nesting or mixed-flock foraging in aquatic ecosystems (Bukacińska et al. 1996, Péron et al. 2010).

While HPAIV affects many species, placing vulnerable and competent host rankings in the context of species' ranges and ecological niches (e.g., wild and domestic overlap; gregarious flocking, scavenging) can refine our understanding of inter- and intra-species viral dynamics, as not all modes of transmission are relevant for all species, nor will all species interact. Though contact and respiratory droplet transmission is possible, HPAIV transmission generally occurs through the fecal-oral route (Blagodatski et al. 2021), where species become infected through shared waterbodies, such as when large numbers of mallards or herring gulls are present on waterbodies overlapping with other waterbird species (e.g., black-crowned night herons). Even species with relatively poor capacity to shed virus (e.g., passerines) may facilitate environmental spread when individuals aggregate in large enough flocks (Root et al. 2022). Additionally, predatory and scavenging species may become infected by consuming infected prey (Günther et al. 2024), such as American kestrels feeding on small passerines (van den Brand et al. 2015) and black vultures

(*Coragyps atratus*; Cunningham et al. 2025) scavenging on conspecifics concurrent with an HPAIV outbreak in lesser scaup and other aquatic birds. In challenge studies, mallards, herring gulls, black-crowned night herons, and house sparrows exhibited some combination of higher infection rates, lower mortality rates, and moderate to high shedding rates. Our results could further benefit from a phylodynamic approach to understanding transmission patterns, specifically using ancestral state estimation to reconstruct transmission chains.

Relating ecological and environmental factors to avian influenza viral dynamics

Identifying transmission risk factors in wild bird populations

The HPAIV transmission risk factors associated with wild populations include the distribution and abundance of wild birds, the prevalence of avian influenza within these populations, and differences across individual species for both factors. There is a strong relationship between the abundance or presence of wild waterfowl and spillover risk (Mulatti et al. 2018, Humphreys et al. 2020, Gierak and Śmietanka 2021). Though historically the abundance of waterfowl has been difficult to estimate in any detail, recent continental-scale spatiotemporal models based on wild waterfowl have alleviated this problem across North America, and increasingly the rest of the world (Humphreys et al. 2019, Fink et al. 2020, Yin et al. 2023). However, waterfowl distributions only describe half of the relevant processes defining risk, as viral transmission can only occur if the species present are carrying viable influenza viruses. As such, several studies have sought to estimate the prevalence of avian influenza in these wild waterfowl across space and time (Kent et al. 2022, 2023), though inference based on waterfowl alone is likely an incomplete representation of virus prevalence on the landscape.

To extend our understanding of the HPAIV system, we identified correlations between disease outcomes and host functional traits. Across systems, exposure risk is heavily influenced by host functional traits, such as dietary preference, distribution range, and behaviors (e.g., migration strategies), which determine interactions with other individuals and viruses in the environment (Worsley-Tonks et al. 2020; Yin et al. 2023, 2024). However, only a handful of studies have been conducted to clearly delineate these relationships for HPAIV. One study found that body mass of avian species was positively associated with the capacity to host HPAIV strains (Yin et al. 2023), while others identified a link between competence and a species' pace of life (i.e., an evolutionary trade-off between investment in survival and reproduction; Harvey and Zammuto 1985, Sæther 1988, Read and Harvey 1989, Healy et al. 2019) in various pathogen-host interactions (Ostfeld et al. 2014, Downs et al. 2019, Becker and Han 2021). For example, waterbirds have a fast life-history pace (high reproductive rate, short time to maturity, short life-span, and large clutch size; Ricklefs and Wikelski 2002) and host a greater number of HPAIV subtypes (Yin et al. 2023, 2024). This distinction is particularly important when contrasting LPAIV and HPAIV; LPAIV rarely causes host mortality, thus poses limited demographic threats to most species, whereas HPAIV can cause massive mortality, posing a substantial demographic threat, especially for endangered species. Species with a slow pace of life (i.e., long lifespan, low reproductive rates, and small clutch size) are therefore at high risk, as a population cannot recover quickly enough following the demographic loss. It potentially leads to a long-term population decline or, in worst-case scenarios, local extinction. In contrast, fast-paced species may be more demographically resilient to repeated mortality events. This difference indicates that pace of life traits are critical for identifying wildlife species that are vulnerable to population-level impacts of HPAIV infections. However, the effects of multifactorial drivers have yet to be explored in depth.

As data availability increases, viral dynamics models can be scaled up to the community level to assess outbreak risk across avian assemblages (Huang et al. 2019; Yin et al. 2023, 2024). Community-level functional trait diversity may strongly influence viral transmission efficiency, particularly for HPAIV, where indirect environmental transmission is substantial (P. Huang et al. 2023, Yin et al. 2023). Communities with less diverse functional traits may experience higher transmission efficiency due to increased spatial and environmental overlap among hosts, as exemplified by efficient HPAIV transmission among waterfowl that congregate in aquatic habitats conducive to environmental viral persistence and fecal-oral transmission (Gelfond et al. 2009, Takekawa et al. 2010).

Identifying spillover risk factors in domestic poultry

Despite the connection between avian influenza-infected wild waterfowl and outbreaks at nearby domestic poultry facilities (Humphreys et al. 2020, Prosser et al. 2024), the mechanisms of spillover and the role of different species remain unclear. Although HPAIV spillover is most often considered in terms of risk to poultry operations, HPAIV transmission from domestic poultry to wild birds occurs less frequently but remains a plausible source of infections in wild populations (Lee et al. 2018, Damodaran et al. 2025) and therefore warrants consideration in risk modeling. The extent of spillover from domestic into wild populations is yet unclear, as sampling around outbreaks has not been prioritized on a broad scale for many avian hosts. There is evidence that animals in and around outbreaks do contract the virus, but the extent and mechanisms of transmission are unclear (Caserta et al. 2024, Damodaran et al. 2025). Phylodynamic approaches to estimate transitions between wild and domestic birds demonstrate that transmission is strongly biased towards introduction into domestic birds, with relatively few inferred spillover events from domestic poultry into wild populations (e.g., 106 versus 4 transitions; Damodaran et al. 2025); though these inferences are limited by available sequence data across hosts and systems and may change as more sequencing data becomes available. The bulk of research exploring IAV transmission to domestic poultry has focused on farm-to-farm transmission (Boender et al. 2007, Scott et al. 2018, Andronico et al. 2019), but there have been several efforts to map the spatial and temporal variation in initial introduction from wild birds to domestic poultry. These efforts include spatiotemporal risk models of China (Prosser et al. 2013), Great Britain (Hill et al. 2019), and the United States (Prosser et al. 2024). All these studies identified that transmission risk occurs at the intersection of both wild waterfowl and domestic poultry operations, and the degree of risk is determined by variation in both wild and domestic birds across a landscape.

The domestic poultry side of this problem includes factors such as location of poultry farms, local wild bird habitat characteristics, differences among farm types, and potential biosecurity measures that could be implemented. However, such data, especially at the local level, are not typically available in the United States. To overcome this hurdle, further models have been developed that combine the larger-scale data available from the United States agricultural census with either distribution models based on environmental variables or artificial intelligence to detect likely poultry facilities from satellite imagery—or some combination of the 2 (Burdett et al. 2015, Patyk et al. 2020, Robinson et al. 2022).

In addition to poultry locations, the type of poultry facilities and the species raised also play important roles in the level of spillover risk. Studies in Europe have consistently shown that turkey farms are at greater risk than chicken farms, with domestic ducks and geese showing variable levels of risk (Gonzales et al. 2010, 2013; Bouwstra et al. 2017; Galletti et al. 2018). Though these patterns could be a result of multiple factors, such as how different species are housed, it appears that they are primarily driven by immunological or physiological differences, which follow similar patterns to those of well-controlled challenge studies (Mutinelli et al. 2003, Aldous et al. 2010, Spackman et al. 2010). Additionally, within chicken production, it appears that broilers are at lower risk than breeder or layer birds—likely because of their short lifespan and high turnover, giving less time for large impacts to occur (Gonzales et al. 2010, 2012; Bouwstra et al. 2017). Finally, poultry kept outdoors appear to be at greater risk than those housed indoors, likely because these outdoor birds have fewer biosecurity protocols preventing their mixing with wild birds or exposure to airborne and waterborne contaminants (Gonzales et al. 2013).

Filling information gaps to improve understanding

Through our holistic data review and analytical approaches, we seek to provide some direction for future research and inform efforts to mitigate the impacts of HPAIV on wild birds. This research not only contributes to the scientific knowledge base but can also provide practical insights for policymakers, public health officials, and wildlife management authorities. Still, with limited current information for many species, such as infection rate, shedding rates, shedding duration, and wild bird mortality rates, our understanding of host roles is largely shaped by limited and historical data, which may not fully capture the current epidemiological dynamics. Given the growing diversity of wild bird hosts and the associated traits that may influence HPAIV dynamics, consolidating information across host species and viral subtypes given more data could further improve our understanding of viral transmission and risk.

Despite a broad understanding of the HPAIV system, there is considerable ambiguity when defining the roles of individual species. Based on our limited dataset, there are relevant gaps in viral response information hindering our ability to inform the current HPAIV system dynamics. We considered 140 species from 32 families within our reviews describing HPAIV prevalence, host response, and host movements, resulting in comparatively sparse datasets (mixture: *n* = 19, NMDS host competency: *n* = 19, NMDS host vulnerability: *n* = 27). In most cases, species were excluded from consideration because of insufficient viral response data from challenge infection experiments; 27 species had at least one data input to describe response to challenge with HPAIV, while only 19 species had information to describe all 6 challenge-related metrics (Figure 3). Overwhelmingly and not surprisingly, challenge study representation was weighted towards species from the Anatidae family, given their role as historical and continued viral reservoirs (Gonnerman et al. 2024, Hayes et al. 2025). Six families were represented by only one species in the dataset, and data were notably unavailable for 23 of the avian families considered. This disparity is contrasted against the dramatically greater numbers of mortality observations in USDA surveillance databases for many of these families, such as Accipitridae (*n* = 727), Cathartidae (*n* = 691), Strigidae (*n* = 248), Pelecaniformes (*n* = 119), and Corvidae (*n* = 118). Challenge study research has not caught up to inform current viral dynamics. Knowledge of these dynamics could be improved by expanding research priorities to describe potential host species' responses. As such, surveillance databases can be used to inform future research targets to adequately inform evolving viral dynamics.

Comparing how species in the limited dataset ranked compared to one another in the phylogenetic neighbor dataset demonstrated how new data may affect rankings. We identified multiple shifts in rankings and groupings for host competency and vulnerability when comparing the limited dataset, which included a smaller number of species with nearly complete data availability, to the nearest neighbor dataset, where viral response data were imputed from the nearest phylogenetic neighbor and constrained to the same taxonomic family. The many changes in species rankings indicated the importance of increased data availability to better inform species roles and rankings. Competent species that retained high-priority rankings (e.g., herring gulls and mute swans) were indicative of well-studied species with established and continuing roles in viral transmission dynamics and were less likely to change their rankings when new information becomes available, given current strain dynamics. By contrast, species that exhibited greater shifts in rankings between analyses were likely deficient in one or more trait inputs by which species were grouped. These results suggested that our ability to assign species HPAIV host response types and determine the prioritization of these species was hampered by the lack of information. This was not unexpected given how rapidly HPAIV system dynamics (e.g., species susceptibility and competence) have expanded, growing the extent of host taxonomic and geographic coverage for clade 2.3.4.4b (Youk et al. 2023).

Challenge studies

A broadened understanding of host responses to IAV will require studying a broader range of host species beyond Anatidae, continuing to test evolving viral strains, and standardizing study methods where possible to enable meaningful comparison across studies. For comparability, future studies can incorporate measuring shedding rates using EID_{50}/mL or EID equivalents, as these are commonly reported in the literature. Together, these efforts will enhance our ability to compare host susceptibility and transmission across diverse avian taxa, and to better understand the responses of free-ranging wild birds.

Challenge studies can inform expectations of host viral response, but this information is limited in many ways. For example, experimental infections are conducted in controlled settings to yield precise data without the noise of environmental variables (e.g., predation, food stress, competition), but the differences in wild and experimental settings can yield dramatically different viral responses (Umar et al. 2016). Using inputs from our analysis as an example, infection and mortality rates observed in challenge studies frequently diverge from the number of subclinical infections or mortalities observed in wild databases. This may in part be due to the previously discussed sampling biases associated with wild detection databases, but challenge studies exhibit similar biases. For example, when animals in experimental studies are infected, they are often directly inoculated with a relatively large dose of virus to ensure infection, complicating estimates of mortality and infection rate. Additionally, the pathway of infection and viral load at exposure can also impact infection, disease progression, and associated outcomes (Gonnerman et al. 2024). Similarly, challenge studies are often conducted with young birds (only a few weeks old) to reduce logistical constraints but with potential impacts on applicability to wild populations. Such issues can be addressed by increased efforts to mimic natural population and transmission dynamics by including broader age ranges and incorporating bird-to-bird and environmental transmission pathways, such as those at shared feeding, nesting, or roosting locations. One option is to assess contact with animals against directly inoculated animals within a study, where naive animals share space, food, and water with infected individuals. While this can exacerbate sample size issues, contact animals that are not successfully infected in their initial trial can be secondarily exposed via direct inoculation to increase sample size (Hall et al. 2011). Studies may also wish to calculate a minimum infectious dose by using multiple direct inoculation doses (DeJesus et al. 2016, Spackman et al. 2019), which may inform what viral loads are necessary to infect animals in wild settings. A number of methods are used to assess viral shedding rates, duration, and infection outcomes, but many are not easily comparable among one another (Gonnerman et al. 2024). Thus, consistency across studies could facilitate comparisons of shedding rates and durations across species and viral subtypes.

Given the noted limitations of wild and experimental datasets, how do we better leverage challenge studies to inform HPAIV–wild bird interactions? Studies of species response to infection could pair controlled challenge studies with targeted field observations, allowing experimental results to validate wild responses and improve their extrapolation. We could then begin to decipher the roles of free-ranging species in viral dynamics such as competency and vulnerability. Challenge studies can incorporate more variables beyond shedding rates and durations to more fully characterize host response, such as behavioral responses (e.g., as conducted in passerine ectoparasite studies; Knutie 2018), physiological responses (e.g., metabolites, electrolytes, proteins), immunological responses (e.g., flow cytometry; Fuess et al. 2021), transcriptomics (e.g., immune gene expression; Videvall et al. 2020), or proteomics (e.g., proteins expressed; Yu et al. 2022). Those inclusions require researchers to consider how the data collected can be used in conjunction with wild data and the host responses of interest. Such efforts will be difficult given the complexities of working in bio-secure facilities but are achievable with appropriate planning. Integrating controlled challenge studies with wild observations provides a framework to refine our understanding of species-level responses and their roles in HPAIV susceptibility and transmission.

Surveillance

Early on, HPAIV surveillance work established waterbirds, particularly waterfowl, as a primary source of HPAIV (Krauss and Webster 2010) capable of spreading virus to other potential hosts (e.g., primarily spillover from wild bird reservoirs to domestic poultry, spillback to wild avifauna and mammals; Olsen et al. 2006, Harvey et al. 2023). As such, surveillance in waterfowl has been robust within the United States, where efforts are led by the USDA along with the United States Geological Survey, United States Fish and Wildlife Service, and the National Flyway Council (USDA et al. 2024). This surveillance program's goal is to detect and identify the spread of HPAIVs, which includes the sequencing of detected H5 and H7 viruses. As such, efforts focus primarily on sampling wild waterfowl across watersheds with sampling effort informed by areas of high waterfowl mixing and by previous years' detections (USDA et al. 2024). As expected, based upon survey design, the USDA wild bird surveillance database for HPAIV during the period January 2020 to July 2025, 89% of the database was populated by waterfowl species (*n* = 112,338 of 126,541). These data were made publicly available through the Bacterial and Viral Bioinformatics Resource Center (BV-BRC) database (Olson et al. 2023), which absorbed the Influenza Research Database (IRD; Zhang et al. 2017).

For non-waterfowl avian taxa, surveillance generally consists of opportunistic mortality detections and reporting, such as HPAIV suspicious carcasses that are sent in for diagnostic testing, some limited capture associated with research projects, and banding programs for specific species. For example, swab sampling during banding of ring-billed gulls (*Larus delawarensis*) at stopover sites was used to identify age-cohort prevalence relationships, while also informing our understanding of viral transmission by identifying the primary shedding route by which virus was excreted (Froberg et al. 2018). Similarly, long-term surveillance programs established for Charadriiformes migrating between North and South America used a combination of fecal collection and cloacal swabs for surveillance, allowing researchers to track changes across time, space, and species (Elsmo et al. 2023). Given the utility of such information for decision making, increased support and capacity for sampling during live-animal captures and a standardized method for reporting could expand knowledge in these non-waterfowl species.

The current United States surveillance plan for HPAIV remains focused on Anatidae, with a continued emphasis on dabbling ducks and the recent addition of diving ducks. Current data reflect a bias towards these species, which are important in transmission and spread, but alone are a less representative output of virus detection and population impacts across the breadth of affected hosts. Further, reporting of mortalities is limited in remote regions or for birds that are less abundant, smaller bodied, more solitary, or with cryptic plumage and less likely to be detected (Fifield et al. 2017). Thus, wild surveillance databases that fail to adjust for these biases, favor larger, overly abundant, and human-associated species (e.g., urban adjacent or harvest species).

Most immediately, surveillance of HPAIV may be expanded by diversifying across host species targets. Limited resources mean that adequately sampling wild populations at risk to HPAIV in a comprehensive manner requires coordination across federal and state agencies, as well as research labs. As an example, research studies that are actively trapping animals could be provided with training and equipment to collect surveillance samples throughout the course of normal field work. We can proactively identify candidate host species using information from challenge studies and wild mortalities (U.S. Geological Survey National Wildlife Health Center 2021, USDA APHIS 2024b) to identify at-risk species that have not yet been appropriately sampled. Longer term, developing a unified reporting system with consistent metadata could strengthen collaboration among research groups, resource managers, and other stakeholders, as current databases are disjunct and either do not include the size of outbreaks, standardized mortality estimates, the number of individuals sampled including negative detections, or including the details of all viral strains, all of which are relevant to transmission dynamics. Further, no broad-scale targeted serological surveillance is in place that can inform previous exposure and seroconversion, the ability to mount an antibody response, and provide information on survival and individuals or populations with detectable immunity across species.

Given the limited resources available for surveillance and the scale of HPAIV transmission, additional options for surveillance may be necessary to collect information. Environmental samples from aquatic habitats (e.g., feces, water, sediment, beach sand) provide a source of samples for monitoring avian influenza and understanding environmental persistence and disease risk (Lang et al. 2008, Poulson et al. 2017, Ramey et al. 2020, Verhagen et al. 2021). Despite the inability to directly correlate environmental samples to hosts, this method removes the limitation of traditional surveillance sampling bias across host species and increases the ability to detect novel viral strains (Coombe et al. 2020, Hood et al. 2021). Environmental transmission may be an important avenue of viral persistence, but viability is dynamic and impacted by local conditions that include the interactions of temperature, pH, and salinity (Brown et al. 2007). Therefore, environmental sampling may serve a complementary role to traditional surveillance of wild birds with potential for early detection of highly pathogenic subtypes when analyzed by genomic sequencing methods (Kuchinski et al. 2024).

Although surveillance is a necessary tool for maintaining an accurate understanding of the current state of the HPAIV system, surveillance alone cannot be adequate for preventing or mitigating disease outbreaks. Instead, surveillance informs management actions, used to minimize uncertainty in the decision-making process (Grant et al. 2017). Information may be used to mitigate the spread of HPAIV among wildlife and reduce negative public health and agro-economic impacts. Monitoring efforts improve our understanding of viral evolution (Blagodatski et al. 2021) and inform the implementation of biosecurity measures (Ramey et al. 2022), planning response strategies, and staging of resources (Machalaba et al. 2015, Verhagen et al. 2021). Surveillance efforts conducted with expert knowledge of IAV prevalence in wild birds and its variability across space and time can improve data usability and ensure that data can be extrapolated (Blagodatski et al. 2021). Surveillance can inform whether a system or species is naive to HPAIV, where HPAIV outbreak risk is highest, and where HPAIV is actively circulating across both fine and broad scales, all of which will greatly impact how management is approached (Langwig et al. 2015).

Animal movements

Potential viral dynamics can be described according to an extensive list of factors that impact HPAIV transmission, spread, and prevalence, but further research can increase understanding and improve descriptions of HPAIV host movements. This includes providing more detailed information on migration and the full annual cycle through the application of advanced tracking technology, expanding research into understudied taxonomic groups, and understanding shifts in behavior as they relate to changes in the environment. For example, as birds are the wild reservoirs for AIVs, we may expect future spatial dynamics of HPAIV to correlate with shifts in seasonal and annual ranges (La Sorte and Thompson 2007, Princé and Zuckerberg 2015) due to changes in weather patterns and more frequent extreme weather events (Horton et al. 2020, 2023) or changing resource availabilities (Socolar et al. 2017).

Although birds within Orders Anseriformes (ducks, geese, swans) and Charadriiformes (gulls, terns, and shorebirds) have received the greatest attention regarding the spread of HPAIV, other understudied taxonomic groups may warrant further consideration. Few studies have investigated the movements of small-bodied species, particular taxonomic groups (e.g., Caprimulgiformes, Columbiformes, Gruiformes, Passeriformes, Piciformes, Podicipediformes, Strigiformes), or species that exhibit irregular movement patterns (e.g., dispersive, irruptive, nomadic; Cottee-Jones et al. 2016, Knight et al. 2018, Scarpignato et al. 2023). From the lens of the ongoing HPAIV H5N1 outbreak, some understudied taxonomic groups (including Accipitriformes, Ciconiiformes, Passeriformes, and Pelecaniformes) may be particularly important to the long-distance spread of virus on a global scale (Yang et al. 2024). Findings from Yang et al. (2024) suggested that birds belonging to the Orders Ciconiiformes, Passeriformes, and Pelecaniformes were associated with more frequent dispersal of HPAIV H5 across Eurasia and Africa during the 2018 to 2023 period.

In addition to basic information on the movements of certain species and taxonomic groups, more detailed information on full annual cycle movements and migratory connectivity could better inform risk mitigation efforts for HPAIV. For example, sea ducks often travel to specific staging areas outside of breeding and wintering grounds (Lamb et al. 2019), which are important for understanding the movement patterns of birds throughout the year and their potential for spreading IAV. Given the large number of Nearctic–Neotropical migrants, large knowledge gaps also exist on the stopover locations and migratory corridors of birds traveling through the Caribbean Islands, Central America, and South America (Bayly et al. 2018). A better understanding of migratory bird movements across multiple seasons and across multiple populations could provide more accurate estimates of migratory connectivity and thus inform viral dispersal at continental scales (McKinnon and Love 2018, Teitelbaum et al. 2023a; see Supplemental 2: Migratory Connectivity and HPAI). Given that few studies have a sufficient geographic scope and sample size to estimate migratory connectivity, these factors can be carefully considered in future studies that aim to address these patterns, potentially via the integration of multiple data sources (McKinnon and Love 2018, Gregory et al. 2023).

HPAIV management

Management options: prevention of outbreaks in wild populations

For management actions to positively impact wild bird species, those tasked with implementing surveillance and response must be properly educated and protected, meaning mitigation and management begin before HPAIV is detected. This includes providing appropriate training for field personnel who may encounter infected animals and educating area and agency management on how to immediately respond to detections. Education can include knowledge of a species putative role on the HPAIV continuum, how to identify symptomatic animals (Cardona et al. 2009, Swayne 2009), potential containment procedures (Simancas-Racines et al. 2023), what personal protective equipment (PPE) is worn to ensure personnel safety (Cai et al. 2009, Occupational Safety and Health Administration 2024) and reduce spread, and how animals are sampled for HPAIV detection (Whitworth et al. 2007, Blagodatski et al. 2021). Given the interactions between wildlife and related sectors (such as public health and the poultry and livestock industry), it may also be relevant to educate partners and collaborators about who can aid in surveillance or would otherwise be negatively impacted if an outbreak occurred. For many agencies already dealing with IAV, monitoring and education have been a priority for over a decade (Youk et al. 2023, Ramirez et al. 2024). The extensive nature of this problem likely requires continuing and expanding these educational efforts to improve the long-term success of any management effort.

Vaccines and viral inhibitors have been developed and tested for avian influenza in different contexts, particularly domestically (Steensels et al. 2007, Bublot et al. 2010, Cagle et al. 2011, Wille et al. 2017), demonstrating some success at reducing mortality and infection in small-scale studies of captive wild populations. However, even if vaccination efforts are scaled up to target vulnerable populations or specific host roles (i.e., superspreaders, superconsumers), 2 major challenges limit the effectiveness of this approach for HPAIV: 1) delivering vaccines to wild, free-ranging populations is logistically impossible (Swayne et al. 2014) and 2) vaccine development must continually adapt to the rapid viral evolution of influenza A viruses (Barnett and Civitello 2020). Given these difficulties, vaccination does not appear currently feasible as a broad control measure for wild populations but may be more appropriate for context-specific application, such as in protecting endangered species (Katzner et al. 2025). Given LPAIV exposure can also elicit natural immunity (Nemeth et al. 2010, Costa et al. 2011, Berhane et al. 2014), monitoring population serology for natural immunity can also inform population vulnerability and guide vaccine-related decision making in a similar fashion.

Although the management of viral transmission risk into wild birds is heavily focused on mechanisms associated with introduction to poultry operations, such as biosecurity practices and rapid response to minimize farm-to-farm transmission, there is also potential for IAVs to spillover from domestic poultry to wild birds. For instance, a mortality event involving 41 wild turkeys (*Meleagris gallopavo*) in Wyoming is believed to have been the result of an H5N1 HPAIV spillover from an infected backyard poultry flock (Malmberg et al. 2023). When considering risk of spillback from poultry, managers may wish to focus efforts on protecting superconsumers who may feed on infected carcasses (Cunningham et al. 2025) and consider requiring protocols regarding the proper disposal of dead poultry and livestock even prior to outbreak detection. Alternatively, managers could instead target management towards interactions with superspreaders, applying measures to limit possible interactions between backyard or free-range poultry with wild bird populations, such as limiting domestic poultry access to spaces or water sources shared by wild birds.

More broadly, in cases where humans are regularly interacting with superspreaders or supershedders, either for research, in the course of work activities, or randomly occupying the same space (Messenger et al. 2014), it may also be necessary to adjust, limit, or cease human activities that contribute to HPAIV spread. For example, food piles and feeders are commonly used for research, business, and recreation, but they may artificially increase the density of animals at a location and facilitate transmission (Reed et al. 2003, Sorensen et al. 2014, Shriner and Root 2020). Alternatively, wildlife research and management often involve the capture or translocation of animals, during which

HPAIV can be transmitted amongst individuals and transported to new areas. In extreme cases it may be necessary to postpone or cease captures, and explicit biosecurity measures could also be implemented to limit the potential for transmission, such as disinfecting surfaces, changing containment units between animals, or wearing and changing PPE during animal handling. Finally, in areas where public access overlaps with high HPAIV risk, actions can range from educating the local community about their level of risk in the hopes of altering behavior (Decker et al. 2012) to completely closing areas with wildlife to prevent potential interactions entirely. As the decision-makers are often subject to public sentiments, transparent decision making and application of surveillance can be used to justify such actions (Fuller et al. 2020).

Management options that support response to outbreaks in wild populations

Active surveillance in wild and domestic birds can allow for rapid identification of novel viral strain emergences and inform managers of potential risks prior to widespread mortalities or transmission events (Duan et al. 2023, Simancas-Racines et al. 2023). However, management options for mitigating and responding to HPAIV outbreaks remain unclear. These decisions will be highly context dependent, as outbreaks can vary in intensity by region, time of year, viral subtype, and host species and population structure (van Dijk et al. 2014, Cumming et al. 2015, Cao et al. 2017, Hill et al. 2019), requiring a broad understanding of available management options and their efficacy.

One approach that has been debated during the current HPAIV outbreak is wild bird carcass removal, with advocates suggesting that removing carcasses of birds believed to have died from HPAIV reduces the amount of virus leached back into the environment and transmission to scavenging species (i.e., superconsumers; Verma et al. 2023). Conversely, opponents of this approach assert that it increases human exposure, requires extensive time commitment, is unlikely to be practical at large spatial scales, and relies on early detection of mortality events (Breed et al. 2012, Harvey et al. 2023). Although carcass removal was a successful response to disease outbreaks like avian botulism (Evelsizer et al. 2010), there is still little research on the efficacy of this method for responding to HPAIV outbreaks.

Beyond the limited feasibility of scaling these actions to more expansive areas, there is also the potential for negative outcomes resulting from inappropriate or excessive application of any one action. Inappropriate application of a given management action has the risk of increasing viral transmission (Prentice et al. 2019) or having no influence on limiting negative outcomes (Bolzoni et al. 2014). Given uncertainty in when to apply response actions and their potential efficacy, it may be better to conserve resources and take no action. For example, not all species will be equally vulnerable if exposed to HPAIV or have the capacity to effectively transmit viruses. Thus, species of lower conservation concern that are more resilient to HPAIV and those with limited ability to transmit and transport HPAIV may be considered lower priority for management action. However, deviations from past trends for a species are possible and warrant consideration should a host species shift in vulnerability or host competence. This requires substantial information on host viral response, such as that available in challenge studies, which does not currently exist for a broad range of species and viral subtypes (also refer to prior review section for HPAIV challenge studies). Additionally, inaction cannot be the primary response from management, as impacts of mass mortality events could dramatically alter population trajectories if left unchecked (Gamarra-Toledo et al. 2023, Wille and Waldenström 2023). As such, the best management option must be flexible, context-specific, and implemented by well-educated and adequately supported personnel.

Integrating science with decision making

The HPAIV system is a complex and cross-sector One Health issue spanning wildlife, agriculture, and human health. Integration of information about individual HPAIV strains and their pandemic potential can help reduce the risk of species spillover events. Through the spring and summer of 2024, dairy cattle in the United States propagated viruses for months with increased spread, likely via transport of cattle and contamination of equipment, resulting in infected cattle across at least 16 states (CDC 2024a). During that time, an increasing number of human infections, including one mortality by 6 January 2025, also resulted from exposure via direct or indirect contact with dairy cattle (CDC 2024b). The increased number of viral infections and broadened host range warn of increased pandemic potential to humans, on top of already highly concerning epizootic potential (Lewis and Beer 2024). These threats to humans could overshadow the conservation crisis presented by continued impacts on wild birds and the associated population declines in a growing number of new species (Croxall et al. 2012). To avoid this, wild bird conservation efforts and surveillance practices can be incorporated across sectors, as many industries are impacted by and can influence viral dynamics.

Currently, decision making is often siloed within independent industries (e.g., avian conservation, agricultural, human health). To address such broadly scoped, multi-objective problems, structured analytical methods provide an avenue for selecting and justifying management decisions in a data-driven fashion (Mitchell et al. 2013, Christie et al. 2022), while also improving transparency throughout the decision-making process (Fuller et al. 2020). A structured analytical framework applied to HPAIV would encourage proactive decision making that considers the range of potential transmission pathways and susceptible hosts (Grant et al. 2017). For example, an efficient and standardized sampling design to guide HPAIV surveillance would maximize our ability to make inference while minimizing resources expended. Because not all species experience equal risks from HPAIV exposure, we can weight sampling design to prioritize highly vulnerable species of conservation concern and highly competent host species that may interact with and spread HPAIV.

A successful disease response will include the ability to adapt quickly to highly dynamic systems, ideally acting proactively before outbreaks become severe. But to be proactive about IAV management decisions, a clear and complete understanding of the system and how it might change are necessary. Additionally, improved support for agencies and institutions to understand maintenance and dispersal of HPAIV could empower each sector to respond according to their interests. Determining unaddressed research gaps is pivotal to inform system dynamics and determine conservation and management priorities. If we produce such a model of viral dynamics prior to outbreaks, less information in real time may be required to make decisions. For the HPAIV system, we seek to describe responses across a broad range of host species, but limited resources have led to uneven sampling that has produced understudied species with high mortality in surveillance databases. Structured analytical concepts, such as the value of perfect information methods (Felli and Hazen 1998, Jackson et al. 2024), can provide a framework to identify the utility of further research for a given species based on what information is already available. Similarly, we could expand research to study undersampled viral transmission pathways, such as environmental spread via infected carcasses or transmission routes during migration. In all instances, a little information can go a long way in establishing whether further efforts are justified.

In addition to integrating science with decision making, better communicating our science to the public can facilitate support for management actions (Bavel et al. 2020, Gupta et al. 2021). However, communicating information about such a dynamic system as HPAIV poses multiple issues, from maintaining an accurate and up-to-date assessment of the system to ensuring public trust as information changes. We can preempt confusion and distrust as information is updated and reported by clearly communicating to the public, industry partners, and decision-makers that we expect dynamics to change over time. Regulations set in one year may not be adequate or applicable in another. Similarly, we can establish reasonable expectations for management outcomes by communicating uncertainty in information used to guide decision making (Peters 2022, Avigad et al. 2023). Public awareness of the risks of infectious disease has been elevated following the COVID-19 outbreak, but distrust and fatigue in issues related to disease have also increased since the outbreak began (Lister and Joudrey 2023, SteelFisher et al. 2023), exacerbated by misinformation on social media (Chowdhury et al. 2023) and impeding our ability to enact adequate responses through public will. A reasonable way to rectify these issues could be a clear and powerful message on what HPAIV risks are and how they might change going forward.

MANAGEMENT IMPLICATIONS

Effective management of HPAIV in wild birds requires translating complex and rapidly changing ecological information into actionable insights and guidance for managers and policy decision-makers. Our synthesis demonstrates that current understanding of HPAIV dynamics in the United States remains incomplete and uneven across taxa, limiting the ability to confidently identify both conservation priorities and host species most influential in viral transmission. While some waterfowl such as mallards, are comparatively well studied, substantial knowledge gaps persist for waterbirds, raptors, and carrion-eaters, which are well represented in mortality databases.

Framing species along an HPAIV host response continuum provides a flexible and integrative approach for interpreting these gaps. By jointly considering host competence and vulnerability, this framework clarifies how species may function as transmitters, recipients, or modifiers of viral dynamics, along with how these roles may shift with ecological context, population density, and viral evolution. These species do not occupy fixed positions along the continuum; instead, host roles are dynamic, reinforcing the need for adaptive surveillance and iterative inference.

Targeted research that links host traits, infection response metrics, movement, and behavior, particularly through complementary field and experimental studies, would substantially improve our identification of species on the HPAIV host response continuum. Surveillance efforts may be most productive when prioritized toward 1) highly vulnerable species of conservation concern, 2) host species driving system dynamics (i.e., abundant hosts with moderate to high competence and low vulnerability), and 3) high-use aggregation and stopover sites that facilitate transmission within and across flyways. Expanded use of environmental sampling, guided by estimates of spatio-temporal risk, may further enhance monitoring efficiency across diverse communities and geographies.

Given the persistence and evolutionary plasticity of avian influenza A viruses, HPAIV management should be approached as a long-term adaptive process. The host response continuum offers a transparent structure for communicating the spectrum of responses. Finally, as we can expect the system to change over time, communication with decision-makers and the public must clearly present our limited understanding of the system, the sources of uncertainty, and how we expect the system and inference to change going forward.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

All studies reviewed in this monograph adhered to relevant regulations and guidelines regarding the ethics of animal welfare.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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