Received: 28 February 2023 | Revised: 31 May 2023 | Accepted: 21 June 2023

DOI: 10.1002/eap.2906

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Waterfowl show spatiotemporal trends in influenza A H5 and H7 infections but limited taxonomic variation

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Funding information
US Geological Survey Ecosystems Mission Area and USDA's Animal and Plant Health Inspection Service, Grant/Award Number: 6000001762; National Science Foundation, Grant/Award Number: 2200310

Handling Editor: Juan C. Corley

Abstract

Influenza A viruses in wild birds pose threats to the poultry industry, wild birds, and human health under certain conditions. Of particular importance are wild waterfowl, which are the primary reservoir of low-pathogenicity influenza viruses that ultimately cause high-pathogenicity outbreaks in poultry farms. Despite much work on the drivers of influenza A virus prevalence, the underlying viral subtype dynamics are still mostly unexplored. Nevertheless, understanding these dynamics, particularly for the agriculturally significant H5 and H7 subtypes, is important for mitigating the risk of outbreaks in domestic poultry farms. Here, using an expansive surveillance database, we take a large-scale look at the spatial, temporal, and taxonomic drivers in the prevalence of these two subtypes among influenza A-positive wild waterfowl. We document spatiotemporal trends that are consistent with past work, particularly an uptick in H5 viruses in late autumn and H7 viruses in spring. Interestingly, despite large species differences in temporal trends in overall influenza A virus prevalence, we document only modest differences in the relative abundance of these two subtypes and little, if any, temporal differences among species. As such, it appears that differences in species' phenology, physiology, and behaviors that influence overall susceptibility to influenza A viruses play a much lesser role in relative susceptibility to different subtypes. Instead, species are likely to freely pass viruses among each other regardless of subtype. Importantly, despite the similarities among species documented here, individual species still may play important roles in moving viruses across large geographic areas or sustaining local outbreaks through their different migratory behaviors.

KEYWORDS

avian influenza, bird flu, disease ecology, H5, H7, influenza A virus, spatiotemporal model, waterfowl

INTRODUCTION

Influenza A viruses in wild bird populations pose risks to the agricultural sector, as well as human health under certain conditions (Clark & Hall, 2006). These risks include direct losses to the poultry industry, in addition to those of culling, response efforts, and trade restrictions (Seeger et al., 2021), as well as health risks associated with exposure of humans in direct contact with infected poultry (Kim et al., 2021). Of particular interest are wild waterfowl, which act as the primary reservoir of low-pathogenicity viruses (Brown et al., 2006) that ultimately become highly pathogenic in poultry farms due to differences in mutation rates and evolutionary trajectories in these aberrant hosts (Suarez, 2000), and whose movement is linked to known spillovers into domestic poultry operations (Humphreys et al., 2020). Moreover, recent changes in avian influenza dynamics have led to new concerns about its impacts on wild bird populations (Harvey et al., 2022). The risk of these outbreaks has motivated much work on the spatial, temporal, and taxonomic variation in influenza prevalence among these waterfowl, with the goal of improving surveillance strategies, risk mitigation, and response planning (Hill et al., 2019; Prosser et al., 2013). As such, it is well established that influenza prevalence peaks in wild waterfowl in the late summer and early autumn, particularly in some dabbling ducks (subfamily Anatinae; Henaux et al., 2010; Keawcharoen et al., 2008; Kent, Ramey, et al., 2022; Olsen et al., 2006).

Immunological work has pointed to the importance of viral subtypes of influenza in dictating both viral ecology and disease risk. Specifically, influenza A viruses contain eight RNA segments, two of which regularly reassort in waterfowl and are central to our understanding of the underlying viral ecology: hemagglutinin (HA) and neuraminidase (NA) surface proteins (Diskin et al., 2020). However, probably due to large amounts of spatial and annual variation, our understanding of the drivers of viral subtype composition remains limited. Taxonomic variation certainly exists, as variation in HA subtypes appear prominent between waterfowl and other taxonomic groups (Pepin et al., 2013; Stallknecht, 2003; Yamnikova et al., 2003), although differences within waterfowl remain relatively unknown. Yet, recent work has demonstrated that annual variation in the common subtypes appears to be cyclic (Diskin et al., 2020; Krauss et al., 2004), and subtype diversity tends to increase as autumn progresses through winter and into spring, with an increase in rare and mixed subtypes later in the season (Diskin et al., 2020). These patterns may be linked to waterfowl movements and congregation; however, how these trends vary among species—as well as finer scale spatial patterns—remain unexplored.

A fuller understanding of the drivers of variation in the prevalence and composition of influenza A subtypes in wild waterfowl will allow for stronger predictions of spillover events into poultry facilities, application to wild bird conservation, and a better understanding of the underlying viral ecology. Although 16 HA and 9 NA subtypes have been isolated from wild aquatic birds (Diskin et al., 2020), of particular interest are the H5 and H7 subtypes, as these are the primary subtypes likely to become highly pathogenic in poultry farms (Olsen et al., 2006). Understanding patterns in the prevalence of these subtypes carries direct management application in our understanding of the spatial and temporal risk patterns, and thus planning mitigation and response strategies.

Notably, current models of spillover risk can only include overall influenza prevalence (e.g., Hill et al., 2019; Prosser et al., 2013), even though only a small subset of these viruses carrys the risk of becoming highly pathogenic in poultry. Several studies have pointed to an increase in the H5 and H7 subtypes in the late autumn and early spring, respectively, in North America (Bevins et al., 2014; Diskin et al., 2020). This rise in the relative prevalence of these two subtypes is consistent with the general increase in rare subtypes as the influenza season progresses (Diskin et al., 2020), and the increase in the H7 subtype may also be linked to migratory blue-winged teal (*Spatula discors*) transmitting the virus to the United States from their wintering grounds (Ferro et al., 2010; Ramey et al., 2014). Moreover, both subtypes appear to be more common in dabbling ducks than in other waterfowl species (Bevins et al., 2014). However, it remains unclear whether these temporal or taxonomic patterns are driven by actual changes in the composition of circulating subtypes or simply cumulative fluctuations in influenza A prevalence across all subtypes.

Here, we used a large dataset surveilling for influenza in wild waterfowl across the continental United States to examine spatial, temporal, and taxonomic changes in the prevalence of H5 and H7 subtypes among influenza-positive waterfowl. This work fills a crucial knowledge gap in the temporal, spatial, and taxonomic variation in the relative composition of these two important subtypes. In doing so, we seek to generate a better understanding of the composition of circulating viruses to better predict spillover events, leading to improved strategies for managing risk and staging response resources, as well as a better understanding of the underlying viral ecology and its potential impacts on wild birds.

METHODS

Surveillance data

Data came from the USDA as part of the United States National Wild Bird Surveillance Program, with sampling conducted between 2007–2011 and 2015–2019 (see Bevins et al., 2014 and USDA, 2017 for methodological details). Sampling efforts were stratified by flyway and species with the goal of maximizing detections while maintaining geographic coverage. Birds were sampled with separate oropharyngeal and cloacal swabs, which were then combined into a single cryovial with brain–heart infusion medium. Samples were tested at the National Animal Health Laboratory Network facilities for influenza A virus using real-time reverse transcriptase PCR (rRT-PCR; Spackman et al., 2002; Spackman, 2020). Positive samples were then additionally tested for the H5 and H7 HA spike proteins using rRT-PCR. Here we focused only on the birds that tested positive for some form of influenza A virus, as we were primarily interested in changes to viral subtype composition. We then subset this database to only include waterfowl species that were well sampled, leaving us with 10 species, each containing at least 450 influenza-positive samples. In total, this resulted in 35,009 samples for analysis (Table 1; Figure 1). We replaced the calendar year with a new variable, biological year, beginning 1 June each year, to better align with the seasonality of the viruses (Kent, Ramey, et al., 2022), as well as the sampling protocols (USDA, 2017).

Data were provided at the county level, and county centroids were used for the spatial coordinates. In general, the use of county centroid where actual coordinates are not available can lead to biases in spatial predictions arising from two distinct lines. First, in analyses that rely heavily on fine-grain environmental predictors, this can lead to a mismatch between the environmental conditions where the data were collected and the centroid of the administrative unit. Second, as counties vary in size, this can impact estimates of the distance over which points are correlated. However, the impacts of analyzing data at county centroids are minimal for models like the one presented here that do not use fine-grain environmental predictors and are instead geospatial and coarse in nature (Barker & MacIsaac, 2022; Cheng et al., 2020; Goovaerts, 2008).

Statistical analysis

To predict the probability of an influenza A-positive bird testing positive for either the H5 or H7 subtypes, we fitted separate sets of candidate models for each influenza subtype using hierarchical spatiotemporal models with integrated nest Laplace approximation (INLA, Rue et al., 2009) using INLA version 20.10.12-1. See Appendix S1 for full mathematical details. This approximate Bayesian method provides a more computationally efficient method for estimating large, spatiotemporal models. We pooled samples by all predictor variables (month, species, county, and year) to set up a binned binomial regression. After preliminary analysis detected overdispersion in the data for both subtypes, the probability that an influenza A-positive bird tested positive for either the H5 or H7 subtypes was modeled as a beta-binomial process, where the probability of success is itself drawn from a beta distribution (Harrison, 2015).

All candidate models contained an intercept, independent and identically distributed (iid) effect of biological year, and two spatial effects. The first spatial effect was a spatially structured latent effect modeled using a

TABLE 1 Number of influenza-positive birds, as well as those that tested positive for the H5 and H7 subtypes for each species.

Common name	Scientific name	*N*	H5	H7
Canada Goose	*Branta canadensis*	463	45	3
Wood Duck	*Aix sponsa*	901	54	13
Blue-winged Teal	*Spatula discors*	3249	177	51
Northern Shoveler	*Spatula clypeata*	2204	187	160
Gadwall	*Mareca strepera*	875	94	14
American Wigeon	*Mareca americana*	913	127	16
Mallard	*Anas platyrhynchos*	18,115	2179	555
American Black Duck	*Anas rubripes*	812	134	20
Northern Pintail	*Anas acuta*	2737	244	44
Green-winged Teal	*Anas carolinensis*	4740	506	147

Abbreviations: H5, number of birds that tested positive for the H5 subtype; H7, number of birds that tested positive for the H7 subtype; *N*, total number of birds that tested positive for influenza.

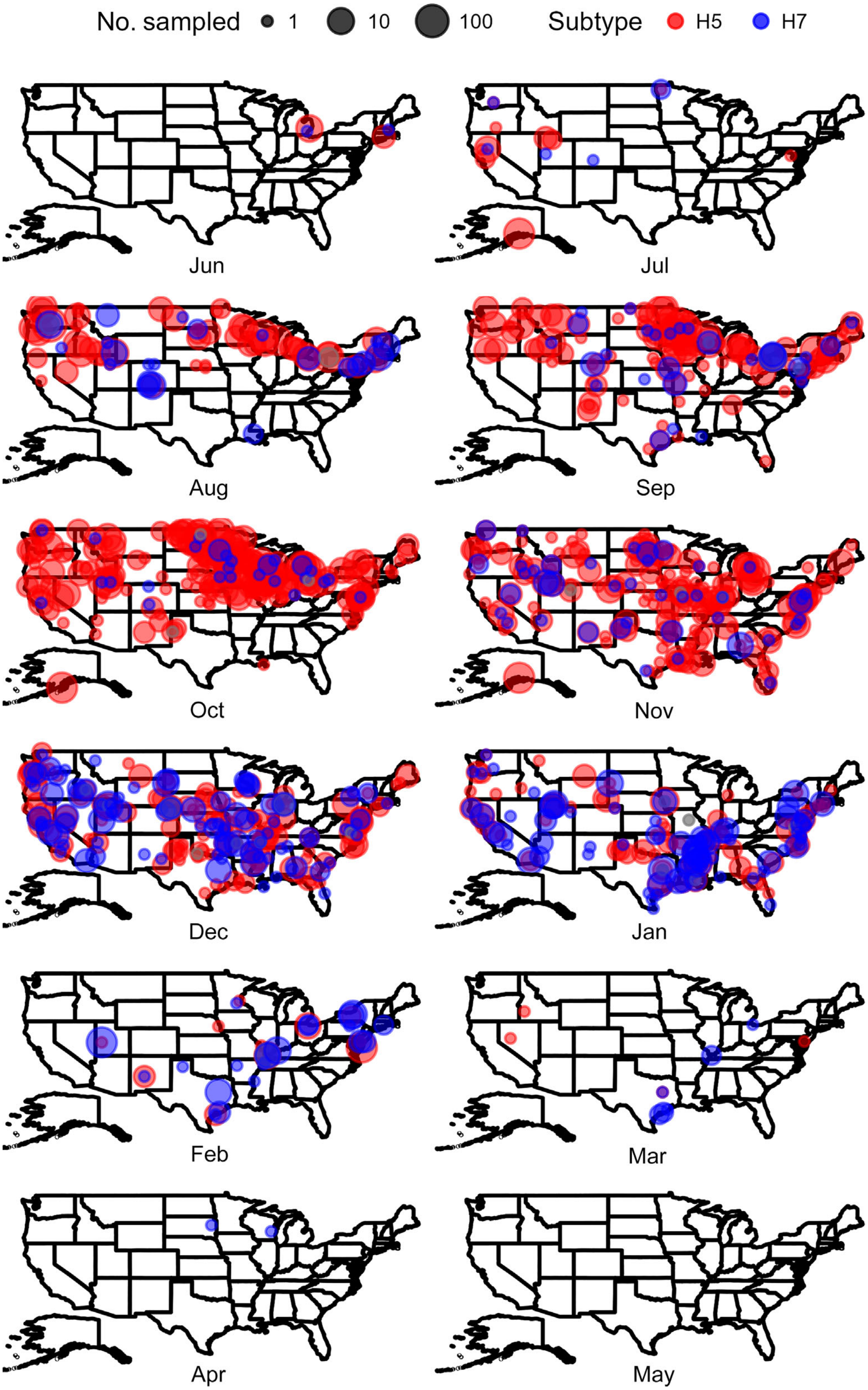

FIGURE 1 Geographic distribution of influenza A-positive samples by subtype.

spatiotemporal stochastic partial differential equation (SPDE) approach to quantify spatial autocorrelation. It used 12 monthly spatial realizations modeled as a cyclic first-order autoregressive (ar1) model to account for correlations in the spatial field between adjacent months (Lindgren & Rue, 2015). This method used a continuous Gaussian random field constructed with a three-dimensional triangular mesh with 8202 nodes, which captured the variation between small counties while retaining computational efficiency (Lindgren & Rue, 2015). Because of the large spatial extent of the data, this mesh was projected into a three-dimensional sphere and scaled to one Earth radius. The second spatial effect was an iid effect of the county to control for small-scale spatial variation, such as the specific locations where birds were sampled or potential variation in sampling methods (Rue et al., 2009).

We then developed four candidate models for both the H5 and H7 subtypes to handle potential species differences. The first of these contained no species effect. The second contained an iid species effect to allow species to differ in the overall prevalence of each subtype but assumed the same underlying seasonal patterns. The third candidate model included a correlated species-specific latent effect of month modeled as a cyclic ar1 process, which allowed species to differ in their temporal trends, while assuming that these trends were correlated (Riebler et al., 2012). Finally, the fourth model fitted a separate month effect for each species, allowing their patterns to fluctuate independently. We compared these two sets of four candidate models using both the Watanabe–Akaike Information Criterion (WAIC) and the inverse sum of the logged conditional predictive ordinate (CPO), similar to a leave-one-out cross-validation (Hooten & Hobbs, 2015).

RESULTS

Model predictions of the proportion of influenza-positive waterfowl testing positive for each subtype for each month at the county level are available online for download (Kent, Bevins, et al., 2022). Overall, 10.7% and 2.9% of influenza A-positive birds tested positive for the H5 and H7 subtypes, respectively. For both the H5 and H7 models, selection methods preferred either the iid or correlated species effects over the models with either no or fully independent species effects (Table 2). Specifically, CPO showed a strong preference for the iid model for both subtypes. WAIC also preferred the iid model for the H7 subtype, but showed some preference for the correlated model for the H5 subtype. However, it should be noted that WAIC is prone to overfitting complex spatial models (Hooten & Hobbs, 2015). Moreover, as the estimated correlation among species was fairly high (0.76), the actual predictions of these two models differed little, so we present the iid model for both subtypes here.

Although these results generally point to limited species effects, with very small, if any, species-specific differences in temporal trends (Figure 2), we did document some species differences in the predominance of these two subtypes after accounting for spatial and temporal sampling differences. Specifically, we found higher levels of the H5 subtype in American black duck (*Anas rubripes*), American wigeon (*Mareca americana*), and mallard (*Anas platyrhynchos*), with lower levels in blue-winged teal and wood duck (*Aix sponsa*). Likewise, we documented an elevated baseline prevalence for the H7 subtype among influenza-positive blue-winged teal and northern shoveler (*Spatula clypeata*; Figure 3).

TABLE 2 Model selection table for different species effects.

Subtype	Species effect	WAIC	CPO
H5			
	Model 1: none	10,470.7	18.8961
	Model 2: iid	10,442.6	−667.533
	Model 3: correlated	10,438.4	−466.388
	Model 4: independent	10,460.5	−499.096
H7			
	Model 1: none	3656.5	−13,881
	Model 2: iid	3591.83	−15,402.5
	Model 3: correlated	3608.89	−14,552.9
	Model 4: independent	3613.17	−13,355.2

Abbreviations: CPO, conditional predictive ordinate; H5, number of birds that tested positive for the H5 subtype; H7, number of birds that tested positive for the H7 subtype; iid, independent and identically distributed; WAIC, Watanabe–Akaike information criterion.

We also documented clear overdispersion, as well as variation in prevalence by biological year and month for both models (Appendix S2: Table S1). Specifically, we found a peak in the prevalence in the H5 subtypes among influenza A-positive birds from October through November, and in the H7 subtype from February through April (Figure 2). However, the combination of low influenza A prevalence and limited sampling in the spring made predictions for this time period more uncertain.

We found clear spatial autocorrelation for both models. During the autumn peak in H5 prevalence, we found elevated levels of H5-positive birds in the Great Lakes region as well as the Northwest (Figure 4a). Likewise, during the spring peak in H7 prevalence, we documented elevated levels of this subtype along the northern Gulf of Mexico moving north along the Mississippi River, as well as in the New Mexico and Utah areas (Figure 4b). These specific trends appeared to be consistent and recurring across years (Appendix S2: Figures S6 and S7).

DISCUSSION

Overall, we demonstrated broad temporal trends in the prevalence of the H5 and H7 subtypes among influenza

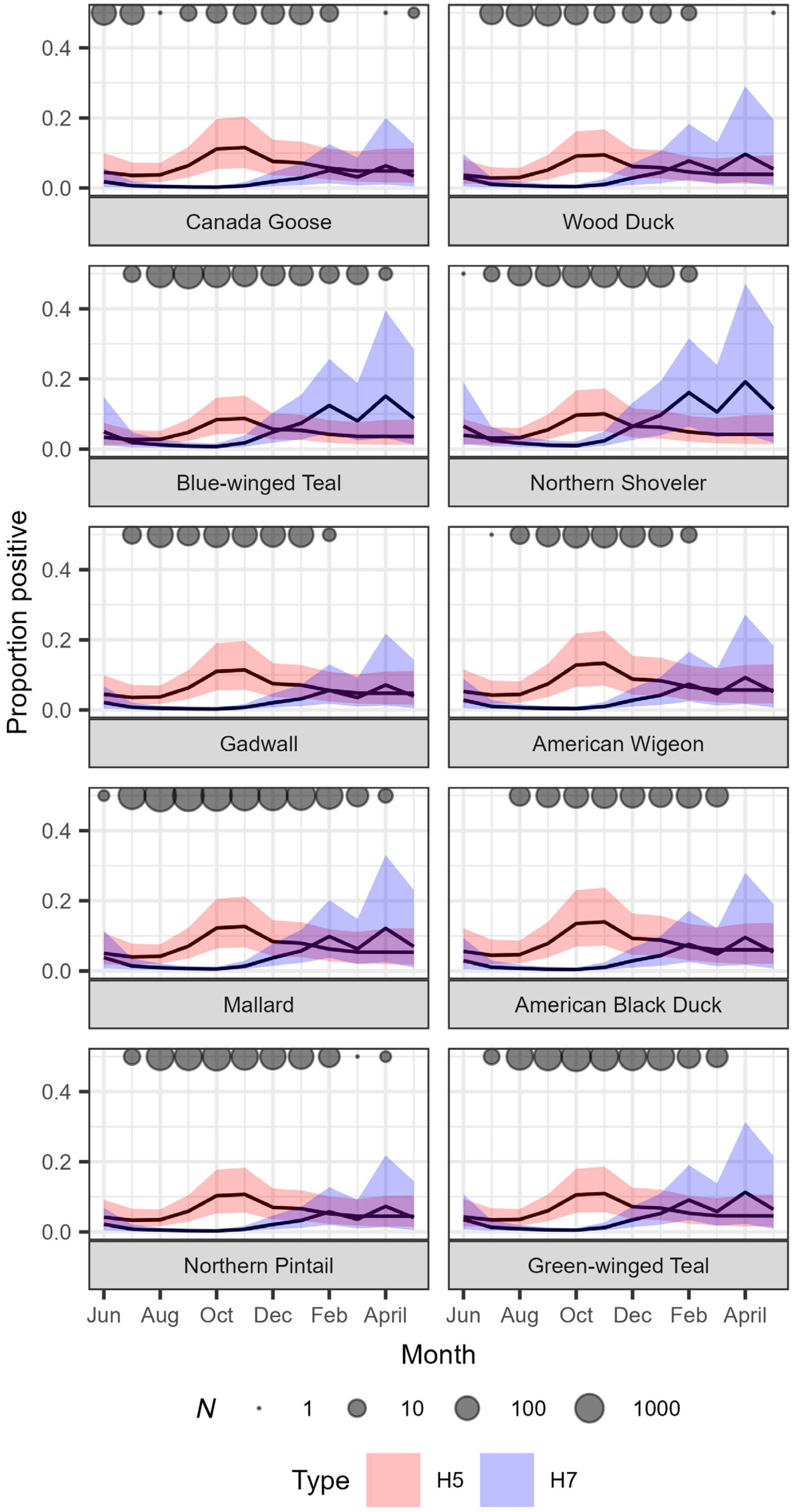

FIGURE 2 Proportion (±95% credibility intervals) of influenza A-positive birds testing positive for the H5 and H7 subtypes by month of year and species. Circles along the *x*-axis indicate the number of birds that tested positive for influenza A virus regardless of subtype. Note that low sample size in spring, particularly April, led to wide confidence intervals for the H7 subtype.

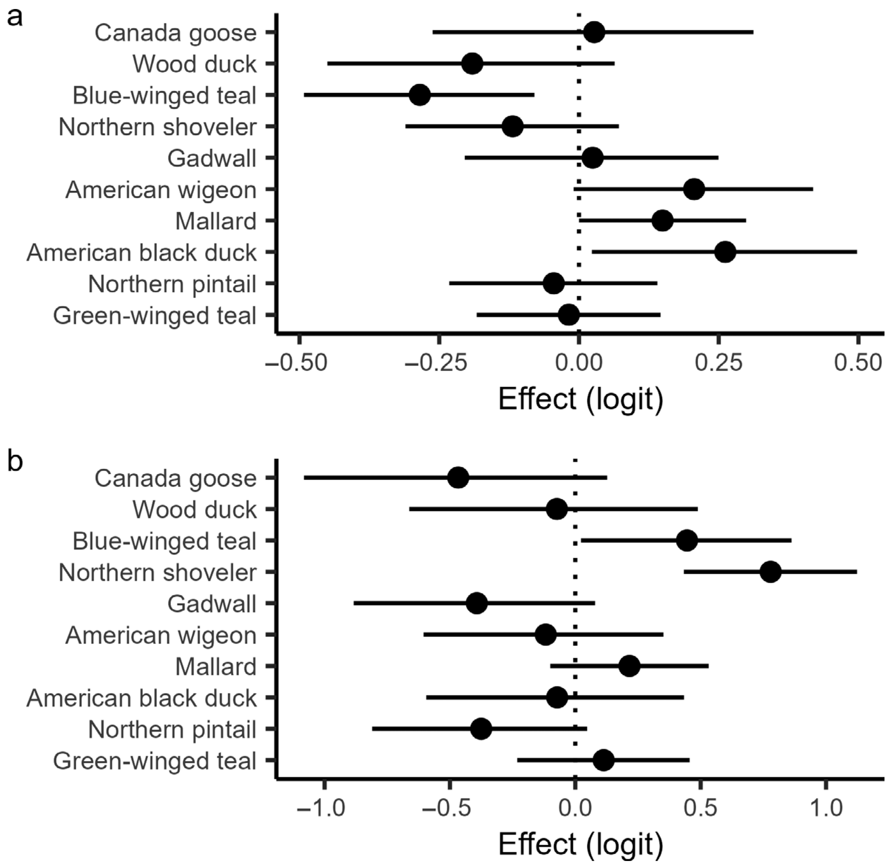

FIGURE 3 Species effect (±95% credibility interval) in logit space for each waterfowl species on the prevalence of (a) H5 and (b) H7 subtypes among influenza A-positive birds. Points to the right indicate elevated prevalence rates.

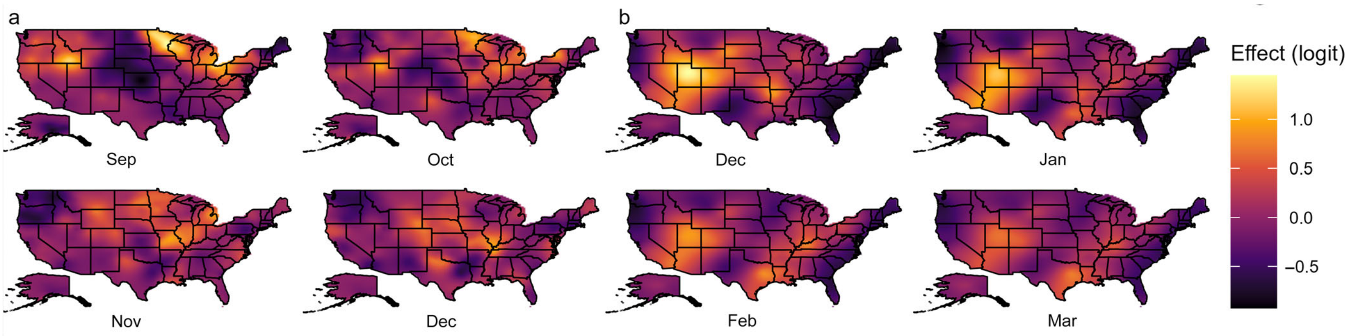

FIGURE 4 The spatial effect, modeled using stochastic partial differential equations with correlated monthly realizations, for the prevalence of (a) H5 and (b) H7 subtypes among influenza A-positive birds. Yellow indicates increased prevalence rate. Only months during which there were elevated levels of each subtype are shown (i.e., September–December for H5, December–March for H7). Plots containing all months and associated standard deviations are available in Appendix S2.

A-positive birds that were largely consistent with past findings (Bevins et al., 2014; Diskin et al., 2020), with the H5 subtype showing an uptick in late fall and the H7 subtype becoming more common in early spring. Additionally, we documented broad spatial trends for both agriculturally important subtypes; however, we found generally limited evidence of taxonomic variation in these trends among waterfowl, finding only small variation in the baseline composition of different subtypes by species and little to no differences in species-specific temporal trends for either subtype. Last, we found some level of overdispersion in the data, where birds sampled at the same time and place were more likely than random to have the same subtypes, probably because they were passing the same influenza strains among each other, as well as variation in relative prevalence by biological year, possibly indicating some periodicity in these patterns (Diskin et al., 2020; Krauss et al., 2004). We have expanded on each of these patterns in the following paragraphs.

As a component of the project, we generated maps at monthly intervals showing the predicted proportion of influenza A-positive waterfowl testing positive for each of these two viruses (Kent, Bevins, et al., 2022). In addition to improving our basic understanding of the underlying viral ecology, these maps may inform management decisions. Much work in recent years has focused on predicting the spillover of avian influenza viruses into domestic poultry operations (e.g., Hill et al., 2019; Prosser et al., 2013). Such models are often based on the number of waterfowl in an area and the proportion of them carrying avian influenza. However, without detailed information on the prevalence of these important subtypes in the literature, such models have been forced to focus only on avian influenza viruses in general, even though the bulk of these pose little risk of becoming highly pathogenic (Diskin et al., 2020). As such, the models and their predictions presented here make data available for improved outbreak prediction and the staging of response resources.

Species trends

Although species certainly differ in their overall rate of influenza A virus infection through time (Kent, Ramey, et al., 2022; Olsen et al., 2006), we found only limited evidence for any species difference in the composition of H5 and H7 subtypes among influenza A-positive wild waterfowl (Table 2). Specifically, CPO preferred the iid model over both alternatives that allowed for different temporal trends by species. Additionally, although WAIC narrowly preferred one of these more complex models for the H5 subtype, this method can be biased toward more complex models in large spatial applications (Hooten & Hobbs, 2015), and the strong among-species correlation led to very small differences between these two models. This contrasts with past work, which has found that viral subtypes differed greatly between waterfowl and other taxonomic groups, such as gulls and shorebirds (Hill et al., 2022; Stallknecht, 2003; Yamnikova et al., 2003), but from our work it appears that these subtype differences are small within waterfowl, at least for these two particularly important subtypes. Notably, some of this may be due to the subtypes examined here, as the work did point to the H5 subtype being general in host susceptibility (Pepin et al., 2013), and it may be that other, less economically important subtypes vary among species.

Notably, this finding of limited differences in temporal trends among species contrasts with large and consistent differences in temporal trends in overall influenza A virus prevalence across these birds (Kent, Ramey, et al., 2022). That is, although differences in behavior, phenology, physiology, or immunology appear to potentially impact overall patterns in influenza A virus prevalence (Costa et al., 2010; Hill et al., 2010; Keawcharoen et al., 2008; Kim et al., 2009; Latorre-Margalef et al., 2017; Olsen et al., 2006), we have little evidence that these differences impact subtype composition, at least as far as the two subtypes examined here are concerned. Interestingly, this large-scale trend is also consistent with previous, local-scale work in Minnesota, where samples of only mallards were sufficient to describe the observed subtype diversity across the whole waterfowl community (Wilcox et al., 2011). As such, it appears that there are limited differences in subtype composition by species, at either small local scales or the continental scale shown here, presumably because these species are easily able to pass these various subtypes among each other (Hill et al., 2016).

These limited differences point to two direct lines of application in surveilling waterfowl for avian influenza. First, as there are some minor differences in subtype composition among species, it may be of use in management applications to focus on the species we demonstrate to have a higher baseline prevalence of these two subtypes. However, contrasting with this, it appears that species are likely to pass various subtypes freely among each other, leading to limited variation in subtype composition among species. As such, managers might surveil for species within broader taxonomic groups (e.g., dabbling ducks, diving ducks, geese, etc.) that are more feasible to capture and sample, with limited concern that they will be missing subtypes that may be more prevalent in species that they fail to sample. Spatial, temporal, and taxonomic sampling strategies will depend on the objectives of the surveillance, for example, early detection of highly pathogenic viruses versus research to understand virus evolution and spread.

As mentioned above, we did document some modest differences in the relative prevalence of these two subtypes by species. Most interestingly, both species in the genus *Spatula* (blue-winged teal and northern shoveler; Sun et al., 2017), showed a higher proportion of influenza-positive individuals testing positive for the H7 subtype compared with the other species. For blue-winged teal, these findings were consistent with published literature showing blue-winged teal with elevated levels of the H7 subtype compared with other species (Diskin et al., 2020; Ferro et al., 2010; Ramey et al., 2014). One mechanism for this pattern in the previous research proposed that long-distance migration of blue-winged teal brought new subtypes to North American sampling areas from Central and South American wintering locations. Long-distance migration is not as distinct in the northern shoveler, which mostly winters in the southern United States and northern Mexico, potentially pointing to some other phylogenetic cause for the higher proportion of birds carrying the H7 subtype, such as differing physiology, behavior, or immunology. Consistent with this phylogenetic hypothesis (similar subtype prevalence in taxonomically related species), we also documented increased levels of the H5 subtype primarily between the closely related American black duck and mallard (Sun et al., 2017). As such, a more complete phylogenetic study, as well as additional immunological work may help to shed light on these species' differences.

Spatiotemporal trends

As expected from past work, we found an uptick in influenza-positive birds testing positive for the H5 subtype during late autumn (Bevins et al., 2014; Diskin et al., 2020). This trend was especially evident in the Great Lakes and Northwest, which are both important staging areas for migrating waterfowl. That is, both regions draw a large number of waterfowl from a wide range of breeding areas. As the mixing of birds from different breeding populations at these staging areas is important for overall viral diversity (Gunnarsson et al., 2012), the mixing also probably leads to an increase in less-common subtypes such as H5 (Diskin et al., 2020) and transmission of those subtypes is further facilitated due to elevated duck densities (Papp et al., 2017).

Also consistent with past literature, we found an uptick in influenza-positive birds with the H7 subtype during the spring (Diskin et al., 2020). Spatially, this increase is strongest along the northern Gulf of Mexico as well as in the New Mexico and Utah areas. These two areas are important flyways for migrating waterfowl, especially the blue-winged teal and the northern shoveler, respectively, both of which were more likely to be infected with the H7 subtype. However, as this uptick was present in all species, not just those two; these species may be important for bringing such viruses into these geographic regions where it is quickly passed among all other waterfowl.

Methodological considerations

The scope of this work was limited by the low number of influenza A-positive birds collected during the spring and summer months. This was a result of two nonindependent sources. First, spring and summer represent a well documented period of low overall influenza A virus prevalence, such that a very large number of birds would have needed to be sampled to obtain even a modest number of influenza-positive birds. Coupled with the low prevalence was the limited sampling effort during that time. Generally, sampling is done with the intent of maximizing detections, so sampling was lower during this time of low prevalence. Additionally, that time period is outside the hunting season, removing hunter harvests as a potential method for data collection; northward duck migration in the spring compounds that problem by complicating any active trapping of waterfowl. As such, we caution against drawing any major conclusions from our findings during those specific time periods, especially in the interpretation of spatial patterns that are more impacted by limited data.

Conclusions

Overall, we documented clear seasonal patterns in the proportion of the H5 and H7 subtypes among influenza A-positive wild waterfowl, as well as provide spatial and temporal estimates of relative subtype prevalence. These model outputs directly inform management regarding potential mitigation and response strategies, as these two subtypes are particularly important for addressing both agricultural and conservation concerns. Moreover, we were the first group to examine differences in subtype composition among diverse waterfowl species on the large temporal and spatial scales, finding only limited differences among species despite their large differences in susceptibility to influenza A viruses.

However, this does not mean that these species play similar roles in the movement of viral subtypes across the continent through migration. As such, additional work may support a better understanding of the role of different members of the waterfowl community in driving the spatiotemporal patterns in these agriculturally and economically important subtypes, including how the phenological, physiological, and immunological traits of these species may influence subtype composition.

ACKNOWLEDGMENTS

The authors would like to thank all those who contributed to the collection of samples included in the US Department of Agriculture database. This research was supported by the US Geological Survey Ecosystems Mission Area and USDA's Animal and Plant Health Inspection Service under Cooperative Agreement 6000001762. Minor support was also provided by the National Science

Foundation (NSF) "PIPP Phase 1: International Center for Avian Influenza Pandemic Prediction and Prevention" (no. 2200310). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are restricted and not available publicly. Wild bird influenza data collected between August 2007 and March 2020 are available from the Wildlife Services National Wildlife Disease Program of the US Department of Agriculture by contacting the National Wildlife Disease Program at nwdpdata@usda.gov.

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SUPPORTING INFORMATION

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

How to cite this article: Kent, Cody M., Sarah N. Bevins, Jennifer M. Mullinax, Jeffery D. Sullivan, and Diann J. Prosser. 2023. "Waterfowl Show Spatiotemporal Trends in Influenza A H5 and H7 Infections but Limited Taxonomic Variation." *Ecological Applications* 33(7): e2906. https://doi.org/10.1002/eap.2906