Predicting high pathogenicity avian influenza H5N1 susceptibility in wild birds

Sara Ryding*[1], Tobias A. Ross[1], Marcel Klaassen[1]

[1]Deakin Marine, School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia
*corresponding author: s.ryding@deakin.edu.au

Abstract

High pathogenicity avian influenza (HPAI) has caused widespread sickness and mortality in wildlife, especially since the emergence of a novel H5 virus belonging to clade 2.3.4.4b in 2021. The ongoing panzootic caused by this lineage has infected an unprecedented diversity of species across the globe, seeming capable of impacting all birds. Here, we analyse ecological and phylogenetic patterns in outbreak notifications of HPAI, and predict host susceptibility to HPAI disease for Australia as the only continent thus far unaffected by this panzootic. We found a significant family-level phylogenetic signal, showcasing that the panzootic is not impacting all birds equally, but ecological traits did not improve predictive power. Using the family-level phylogeny, we predict that families of Australian seabirds, shorebirds, and waterbirds will be most susceptible to HPAI once it arrives on the continent. Our results provide an empirical indication of species susceptible to HPAI H5N1, which can be used to direct monitoring efforts and disease management globally. With special reference to Australia, our predictions can be used alongside conservation status and species-specific information to inform preparedness activities, monitoring, and response upon incursion.

Keywords

Avian influenza; HPAI H5N1; host susceptibility

Introduction

High pathogenicity avian influenza (HPAI) has caused problems for poultry and wildlife for decades, causing significant financial and conservation harm. Low pathogenicity avian influenza (LPAI) viruses are often associated with wild waterfowl, and particularly ducks, and have occasionally evolved into HPAI viruses following spill over events into poultry[1]. HPAI has particularly surged into focus since 2021 due to the emergence of a H5N1 virus belonging to clade 2.3.4.4b that is referred to as HPAI H5N1[2,3]. The current panzootic caused by this HPAI H5N1 virus is unprecedented in scale, having spread to every region except Oceania (including Australia and New Zealand). The virus has caused large scale mortalities in poultry and wild birds, and has increasingly also spilled over into mammalian wildlife and livestock[3-5]. HPAI H5N1 has led to mass mortality events in wildlife and cause for conservation concern in some impacted species. For example, HPAI H5N1 is associated with 60% reductions in both northern gannets in the UK[6] and Dalmatian pelicans in Greece[7], and a 91% mortality rate of Caspian terns in Kazakhstan[8]. At the same time, the spread of the virus is also increasingly facilitated by some of these wild bird species. The HPAI H5N1 panzootic is set apart by increased host promiscuity, no longer being highly adapted specifically to poultry (e.g.[9]) and spreading geographically via far-ranging waterfowl, seabirds, and potentially other wild bird species[10-13]. As such, understanding the new disease landscape for this virus, and notably what species are vulnerable to infection and may play a role in the maintenance and dispersal of the virus is of considerable importance, both to understand why HPAI H5N1 has had such drastic impacts on diverse wildlife and to be able to sketch this panzootic's future trajectory.

HPAI H5N1 has now been detected in over 400 different avian species during the current panzootic[5,14]. Presence of LPAI, from which HPAI evolves, has a strong phylogenetic signal in wild birds[15], meaning avian influenza is more prevalent in certain closely-related clusters of species. Notably, there is phylogenetic signal of LPAI across different orders (with major reservoirs in waterfowl [Anseriformes], followed by shorebirds [Charadriiformes]), but with distinct variation remaining across families and species within orders[15]. However, how well that phylogenetic signal is preserved in the current panzootic is not well understood, and is potentially very different given the diversity of birds currently impacted. The apparent expansion of hosts from previous clades to the current HPAI H5N1 clade 2.3.4.4b impacts the predictability of its epidemiology, and notably our understanding of which species may be severely impacted by HPAI H5N1 as it spreads across the world.

Transmission of HPAI H5N1 within and between species might also depend on an individual's contact with the transmission pathway, i.e. how exposed they are to the virus. HPAI transmission occurs through respiratory tracts and faecal-oral pathways, which can take place directly through interaction with faecal matter or indirectly through interaction with contaminated water, where the virus can persist for a long time[16,17]. Colony breeding, and specific colony traits such as distance between nests, have also been implicated in HPAI H5N1 spread[16,18]. Based on infection patterns in predatory birds and mammals, HPAI H5N1 is also capable of spreading via consumption of infected birds[1,19] and potentially via kleptoparasitism[20]. These distinct transmission pathways suggest specific ecologies that increase the likelihood of birds encountering the virus; association with water, likely contact with faecal matter, dense flocking behaviour, and scavenging or predation are all likely to increase the probability of a species encountering HPAI H5N1[21]. However, empirical testing of these ecological traits that might increase virus exposure across known cases of H5N1 are generally restricted to certain regions (e.g.[18,21,22]), and thus their generality is poorly understood. Improved understanding of how ecological traits can increase disease exposure will furthermore improve our predictive power of which species are likely to be impacted once (or 'if') HPAI H5N1 reaches the last region it hasn't infected, Oceania (including Australia and New Zealand), and other more isolated parts of the world that have so far escaped exposure to the virus.

In this paper, we evaluate the influence of ecological traits and phylogenetic relationships on species' HPAI notifications and use this to predict susceptibility to HPAI disease of naïve, Australian species. We analysed notifications of HPAI in wild birds reported to the World Organisation of Animal Health (WOAH) across the world since the start of the panzootic as our indicator of susceptibility to disease. Using phylogenetic generalised linear mixed models, we modelled notifications of HPAI H5N1 in wild birds against multiple predictors: a family-level phylogeny and ecological traits that might influence disease exposure (habitat, diet, and congregation behaviour). Following model selection, we predict HPAI H5N1 disease susceptibility in Australian birds, who remain unexposed to the current panzootic. Here, our measure of "susceptibility" is the predicted number of HPAI notifications, which is modelled based on HPAI notifications to WOAH.

Methods

To model factors predicting HPAI H5N1 notifications in wild birds, we used the WOAH World Animal Health Information System (WAHIS) database of HPAI notifications. WOAH member countries are expected to submit information on a range of animal diseases, and for each disease notification must provide information on the number of outbreaks and cases, as well as biosecurity measures taken[23]. An HPAI notification in the WAHIS database can represent a) a notification of an HPAI detection in an environmental sample from the recorded wild bird species, b) a notification of an HPAI detection in the species, but where the individual had no obvious or reported clinical signs of sickness/death, and c) a notification of HPAI in sick and dead wild birds of the reported species. Importantly, each notification may represent a single bird or multiple birds from a single species. Therefore, by using 'notifications' rather than 'number of impacted birds' as our input data, we avoid overrepresentations from extreme mass mortality events. While WOAH members are expected to submit notifications on HPAI outbreaks, there is likely a certain amount of underreporting of HPAI to the database[5] which may lead to certain biases. For example, HPAI notifications to WAHIS correlate with human density[5], since diseased birds are more easily observed where there are people. Similarly, it has been found that large-bodied species are more likely to be detected with HPAI because they are easier to observe than small species[22]. Furthermore, HPAI notifications are likely to largely reflect instances of diseased birds, meaning infected but apparently healthy birds are likely to be underreported. We did not filter the dataset to only include notifications where birds died. However, active monitoring is less common in WAHIS reporting than passive monitoring (where testing is done in response to visible disease), thus most notifications include diseased and dead birds (only 3% of notifications reported 0 dead birds). While there is likely underreporting that has important implications for the biases inherent in the dataset, the WAHIS database still provides a minimum indication of HPAI notifications (and may therefore underestimate, rather than overestimate, HPAI events). The database was accessed on 16/02/2026 and filtered to only include notifications of outbreaks reported in wild birds of known species since October 2021. In 95% of the cases, the subtype of the HPAI notification was evaluated and established to be HPAI H5N1 (remaining being H5 or unknown). We therefore assume that the majority (if not all) notifications used in our study relate to HPAI H5N1, but will use the phrase ‘HPAI’ to capture the possibility of other subtypes. It should be noted that WOAH bears no responsibility for the integrity or accuracy of the data, including but not limited to any deletion, manipulation, or reformatting of data that may have occurred beyond its control.

HPAI H5N1 has spread through different world regions since 2021, with more severe impacts in different regions at different times. To account for the spatial spread of HPAI across large regions, we grouped HPAI notifications by region. Region was determined using the ‘countrycode’ package[24] in R, where each country was grouped to one of seven regions: ‘East Asia and Pacific’, ‘South Asia’, ‘Middle East and North Africa’, ‘Sub-Saharan Africa’, ‘Europe and Central Asia’, ‘North America’, ‘Latin America and Caribbean’, and ‘Antarctica’. In the resulting dataset, we had number of HPAI notifications per species per region. The full spatial distribution of HPAI notifications in wild birds made to WAHIS in our dataset is show in Figure 1.

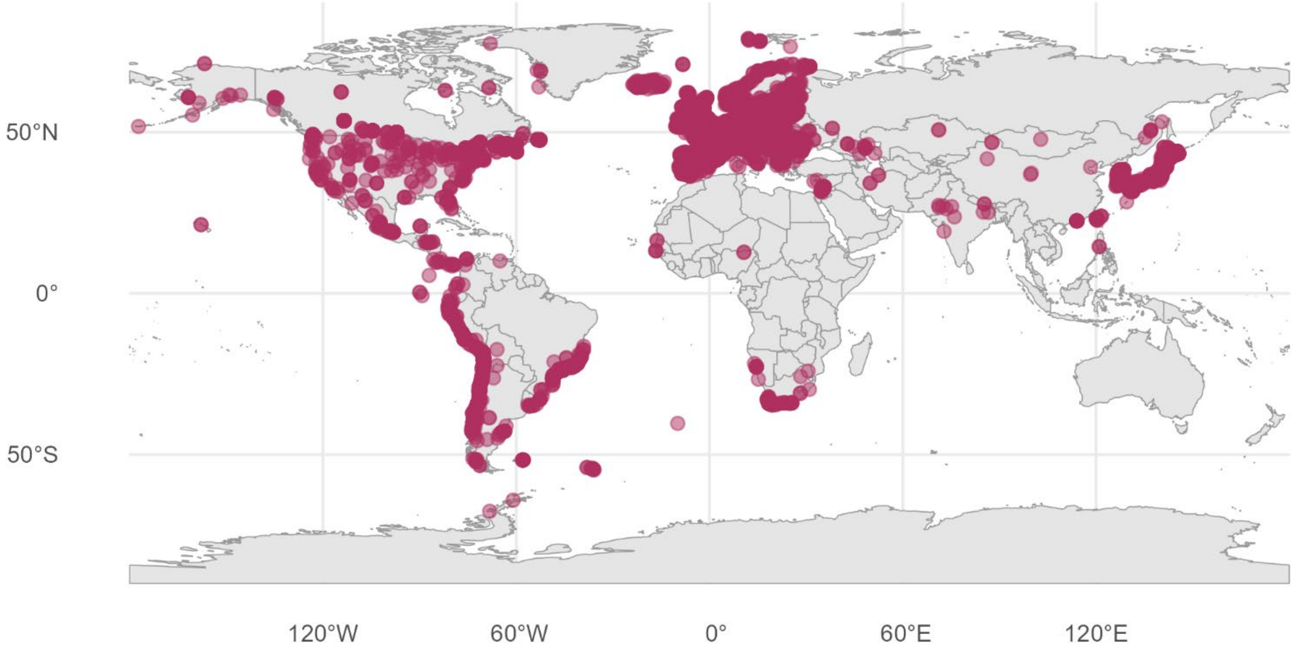

Figure 1: Map of WAHIS HPAI notifications in wild birds. Each dot represents the reported location of a HPAI notification, and can represent one or several birds of a species. There is likely underreporting of HPAI notifications to WAHIS, but the data represents the minimum HPAI notifications. The data was accessed on 16/02/2026 and filtered to include notifications after October 2021.

Because of the links between disease transmission pathways and ecological traits like aquatic lifestyles, certain feeding ecologies, and tendency to congregate, we modelled how ecological traits might influence HPAI notifications in wild birds. Initial ecological categorisations of habitat and trophic niche were obtained from Avonet[25]. In our analyses, we wanted to avoid categorisations that were too narrow (e.g. differentiating between frugivores and granivores) or perhaps arbitrarily differentiated between species with otherwise similar ecologies (e.g. denominating the Common Merganser as inhabiting "riverine" habitat, but other mergansers as "wetland"). Therefore, we modified some habitat and trophic niche categorisations based on information in Birds of the World[26], and broadened the groupings. We thus had three categories for habitat: Terrestrial, Freshwater, and Coastal/Marine, and four categories for diet: Predators (including vertebrate predators and scavengers), Piscivores, Plant-based diets (including aquatic and terrestrial plant material), and Omnivores (including any species that were both predators and plant-based feeders, and invertebrate predators as these often also take plant matter). We used BirdLife's list of congregating birds as our initial starting points for whether species were known to congregate or not (Y/N), and supplemented this with information from Birds of the World[26]. For a full list of species and our ultimate ecological categorisation for these species, see Supporting Information Table S1.

To predict HPAI disease susceptibility in Australian birds in the event of HPAI H5N1 incursion into Australia, we used the BirdLife Working List of Australian Birds dataset (https://birdata.birdlife.org.au/whats-in-a-name) to generate a list of Australian bird species. The list was refined to exclude rare vagrants and uncommon non-native species. Similar to how we treated the WAHIS dataset, we used Avonet's and BirdLife's ecological data on habitat, diet, and congregation as starting points, with refinement and broadening of categories to generate matching ecological traits. The full list of Australian birds we used, their ecological categorisations, and their IUCN status can be found in Supporting Information Table S2.

Statistical analyses

All analyses were conducted in R version 4.4.0[27].

To model HPAI notifications in birds, we used a phylogenetic generalised linear mixed model (GLMM) in the 'brms' package[28]. In all the following models run in 'brms', we used the flat default priors and ran models for 5000 iterations, with 600 iteration warmup and a thinning interval of 5. Model convergence was assessed by visual inspection of chains and by posteriors predictive checks of the models (using the 'pp_check' function). We used a Poisson distribution of the number of HPAI notifications per species per region (region defined using the 'countrycode' package as outlined above), controlling for region as a fixed effect and running the model under a phylogenetic framework. For the phylogeny, we used the family-level phylogeny from Kuhl et al[29]. We used family, rather than species-level phylogeny to avoid reporting biases for more common species, when species in the same family are likely to share similar ecological traits and immune system architecture. This was especially relevant for our next step, outlined below, wherein we used the model of HPAI notifications to predict HPAI H5N1 disease susceptibility in Australian species (we wanted to avoid drastically uneven outbreak notification estimates for Australian species in the same family, but where some species were closely related to a species with high HPAI notifications). We built upon the phylogenetic GLMM to include the ecological traits of species: habitat (N = 3 categories), diet (N = 4 categories), and whether the species is known to congregate (Y/N). The models did not include any offsets. We fitted three models that had one ecological predictor (habitat, diet, or congregation) in addition to region as fixed effects, and then an additional model that included all 3 ecological predictors and region. We evaluated model fit of these against the null, region and phylogeny-only model using leave-one-out (LOO) cross validation information criterion (IC), which is interpreted similarly to AIC where low values are associated with better models.

The next step in our analyses was to predict which Australian species may be susceptible to HPAI H5N1 once (or 'if') it arrives in Australia, based on patterns of HPAI notifications elsewhere in the world. We used the HPAI notification data to predict numbers of HPAI notifications in Australian birds, and use this as our metric of predicted susceptibility to disease from HPAI H5N1. Most (~97%) of HPAI notifications in the WAHIS database since October 2021 report deaths for species that have outbreak notifications, which means that our predicted susceptibility is also linked to a species' likelihood of experiencing sickness and death. To predict susceptibility to HPAI H5N1, we first added the Australian bird families to our above phylogeny[29], thus resulting in a phylogeny with the families in the WAHIS database and the Australian families. Using the 'castor' package[30], we predicted HPAI notification likelihood onto the Australian species. This was done using hidden state prediction via phylogenetic independent contrasts, using the family-level phylogeny with both known and unknown HPAI notifications (wherein known HPAI notifications were expressed as an average per family). Through this, we retrieved predicted HPAI notifications for Australian bird families, which we interpreted as their predicted susceptibility to disease from HPAI H5N1.

Plots were made using 'ggtree'[31] and 'ggplot2'[32]. Lastly, we extracted IUCN Redlist status for Australian species using the 'rredlist' package[33], to ascertain the conservation status of any species predicted to be highly susceptible to HPAI and thus highlight species that may be at greater risk due to pre-existing vulnerabilities or due to other reasons than vulnerability to HPAI H5N1.

Animal ethics statement

Our data is sourced from the WOAH WAHIS database of global HPAI notifications in wild birds. Therefore, our analysis is conducted on a pre-existing dataset with no new data collected for the purpose of this study. We have no permit details to report.

Results

When analysing notifications of HPAI in wild birds since October 2021 using the phylogeny-only model, we found a statistically significant phylogenetic signal (Pagel's λ: 0.56, 95% CI: 0.22 – 0.84). There were predominantly high numbers of total and average HPAI H5N1 notifications amongst Anatidae (ducks, geese, and swans), Laridae (gulls, terns, and noddies), Sulidae (gannets and boobies), and Gruidae (cranes). To a lesser extent, crows and ravens (Corvidae), birds of prey (like Falconidae and Accipitridae), and other seabirds (like Pelecanidae [pelicans] and Alcidae [auks]) also had higher numbers of HPAI notifications (Figure 2).

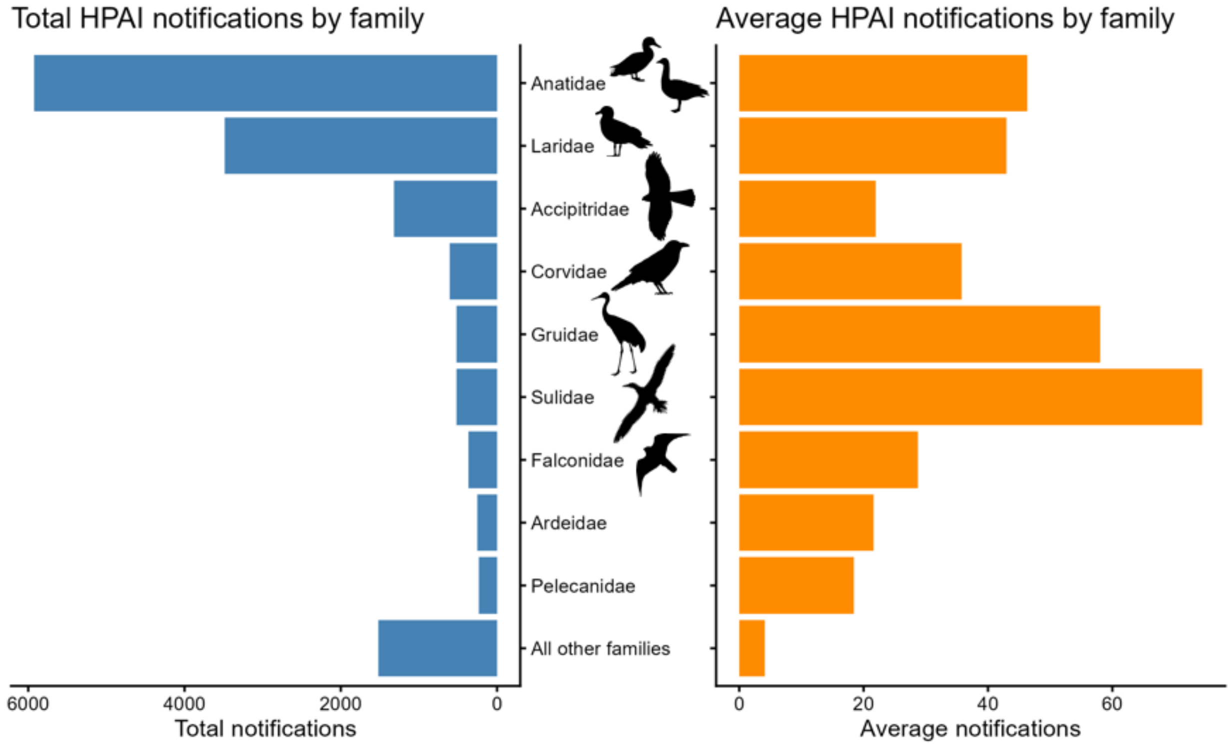

Figure 2. HPAI notifications in wild birds 2021 – 2024. The left panel shows total HPAI notifications made to WOAH WAHIS per family, while the right panel shows average HPAI notifications per family. A few key families are highlighted by inclusion of bird icons from phylopic.org, going down from the top: Anatidae, Laridae, Accipitridae, Corvidae, Gruidae, Sulidae, and Falconidae.

Using leave-one-out (LOO) cross validation, we compared the fit of this null, region and phylogeny-only model and that of the ecological traits models. There were 4 models with ecological traits, where 3 models consisted of a single ecological trait (habitat, diet, or congregation) and a fourth model that included all three ecological traits (see Table S3 for summary statistics of all models). All four of these models included the phylogeny and region (see Methods). There was substantial overlap in the standard errors of the LOO ICs computed for the models, which means that the additional variables in our ecological models did not significantly improve model fit over the null, phylogeny-only model (Figure S1;[34]). Therefore, we present results for the simpler, phylogeny-only model.

When predicting Australian species' HPAI H5N1 disease susceptibility (defined as their predicted HPAI notifications), the predominant groupings of predicted notifications were similar to that of the training model (Figure 3). Based on global HPAI notification data since 2021 and the family-level phylogeny, the highest predicted HPAI H5N1 susceptibility was predicted for Australian Sulidae (gannets and boobies), followed by Gruidae (cranes), Anhingidae (darters), Anatidae (ducks, geese, and swans), and Laridae (gulls, terns, and noddies). Specifically, the model predicted 74 notifications (i.e. HPAI detections in environmental, living, or dead bird samples) of HPAI in Sulidae family members, followed by 58 in Gruidae, 51 in Anhingidae, 46 in Anatidae, and 43 in Laridae family members. Other Australian bird families, like Pelecanidae (pelicans), Corvidae (crows and ravens), and Accipitridae (falcons, hobbies, and kestrels), were also predicted to be susceptible to disease. Furthermore, some families endemic to Australia, such as Anseranatidae (containing the magpie goose – *Anseranas semipalmata*), were predicted to be moderately susceptible to HPAI with a predicted 26 notifications. Predicted HPAI notifications for all Australian bird families in our list are reported in Supporting Information Table S4.

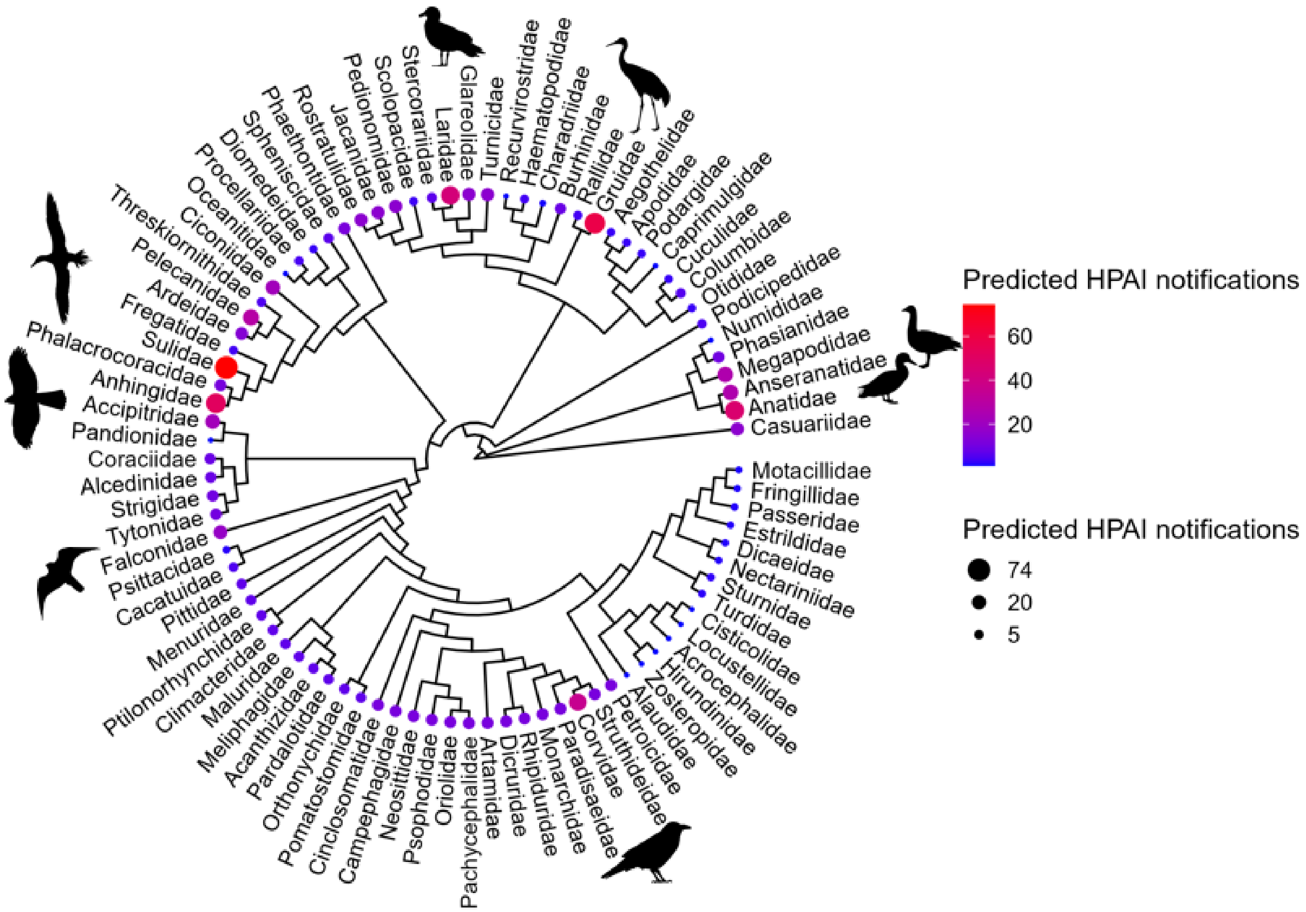

Figure 3. Predicted HPAI H5N1 susceptibility for Australian bird families. Each tip denotes a family, with the size and colour of the tip representing the predicted number of HPAI H5N1 notifications. Key families are highlighted by inclusion of bird icons from phylopic.org, going clockwise from the top: Laridae, Gruidae, Anatidae, Corvidae, Falconidae, Accipitridae, and Sulidae.

Discussion

HPAI H5N1 2.3.4.4b has caused a panzootic of unprecedented scale[5], but has not yet spread to Australia[4]. Here, we modelled HPAI notifications as a function of ecology and family-level phylogeny, finding that family-level phylogeny best explains number of HPAI notifications. The importance of host phylogeny in explaining avian influenza prevalence has been previously noted for low pathogenicity viruses[15] and for HPAI H5N1 in different regions (e.g.[10,12]), which we now expand for a global dataset of HPAI. Furthermore, we use phylogeny to predict HPAI notifications in Australian birds (including for Australian endemic birds), as a metric of susceptibility to HPAI H5N1 infection and resulting disease once (or 'if') it reaches the continent.

While transmission of HPAI H5N1 is believed to link to ecological traits related to e.g. (aquatic) habitat choice, (dabbling) foraging strategies, predation, and congregation, including these ecological traits in our model did not significantly improve model fit. However, we do not believe the support for our phylogeny-only model means that ecological traits are not important – rather, there are specific traits as well as combinations of traits yielding scenarios of probable disease transmission that are likely captured by the family-level phylogeny. For example, Anatidae (ducks, geese, and swans) have a high number of HPAI notifications globally and are among the families predicted to be most susceptible to disease from HPAI H5N1 in Australia, likely due to their aquatic lifestyle. Conversely, we hypothesized terrestrial birds to have lower HPAI notifications due to largely avoiding contact with HPAI virus contaminated water, but many birds of prey (which have high HPAI notifications) are terrestrial predators. This specific interaction between diet and habitat may be important in predicting HPAI notifications, but it is captured already in the family-level phylogeny, as such traits tend to be shared across members of a family and even entire orders. The drawback of our approach is that the predicted HPAI notifications are generalised across species in a family. Generalising across families may be especially penalizing for species that are ecological outliers compared to others within their family. For example, our study predicts high HPAI notifications for the Australasian wood duck (*Chenonetta jubata*), despite its ecology differing from other ducks (it is an exclusively grazing duck, while many other ducks engage in filter feeding and dabbling) and its previous identification as an outlier in having low LPAI virus and seroprevalence[15]. Similarly, subtle differences in the type of congregation behaviour can seemingly drive some differences in HPAI susceptibility between closely related species, such as the relatively low effect of HPAI on little terns (*Sternula albifrons*) compared to other terns, which was attributed to bigger spacing between nests and their tendency for single-species colonies[35]. Despite such exceptions, our predictions can serve as an initial guideline of species likely to be impacted by HPAI H5N1, with additional information such as species' conservation status, population size, and a variety of site- and species-specific factors used to assess potential local impacts.

In our prediction of HPAI H5N1 susceptibility in Australian birds, we define susceptibility as the predicted number of HPAI notification for a taxonomic family (where high numbers of predicted HPAI notifications is interpreted as high susceptibility to disease; with 74 HPAI notifications in Sulidae being the highest score). This modelling is based on data of “outbreak notifications” from WOAH WAHIS since October 2021 (the onset of the current panzootic), where most (~97%) species with notifications also have reported deaths from HPAI. As such, assuming that notifications to WOAH WAHIS is strongly correlated with disease and/or death, our predicted HPAI H5N1 susceptibility largely reflects how easily different birds become infected and subsequently die of HPAI. However, our susceptibility predictions largely ignore the role of different birds in maintaining and spreading HPAI H5N1, since different species might survive (and some may indeed not die from infection) and carry the virus for different lengths of time. For example, bald eagles (*Haliaeetus leucocephalus*) had higher HPAI H5N1 seroprevalence (indicating higher survival rate) than other birds of prey[36], and anti-H5 antibodies in seabird eggs were higher in common eiders compared to other seabird species (such as gannets, which suffered HPAI-related mass mortality events[37]). In the current HPAI panzootic, recent research has shown that the host dynamics of H5N1 differs between virus genotypes[38], showcasing the wide range of birds capable of contributing to the spread of HPAI and that the reservoir community can change rapidly. Furthermore, migratory and partially-migratory birds are likely to have a significant role in sustained transmission of HPAI H5N1 to other birds, as has been found in other regions[10,12,13]. This suggests that species can play different roles in maintenance and spread of HPAI H5N1 after exposure to the virus, which is important to consider when predicting HPAI H5N1 susceptibility. How HPAI H5N1 spread may look like within the Australian continent is further complicated by the often nomadic movements of Australian waterfowl as they move in response to ephemeral wetlands[39].

In this study, we used a family-level phylogeny to avoid biases associated with particular outlier species. Our approach may still carry some inherent biases, for example if a family is very speciose, very abundant, or contains very commonly sampled species. However, when comparing the mean number of HPAI notifications per family to the number of species in that family, the correlation was low (R^2 = -0.06), meaning it is unlikely biases related to number of species in a family are entirely driving our predictions. Indeed, because we analysed the data using the family-level phylogeny that considers HPAI notifications across a family (rather than just the total), we avoid some of the exaggerated total HPAI notifications associated with very speciose and common families like Anatidae and Laridae (Figure 1). However, it may also be argued that this introduces its own form of bias, if it "punishes" the HPAI susceptibility predictions for speciose and common families (hence why our model predicts Sulidae, rather than Anatidae, to be the most susceptible Australian family; Figure 1). It is also worth noting that our approach is inherently biased by people sampling for and reporting notifications of HPAI H5N1, where real numbers of HPAI H5N1 likely exceed recorded notifications by an order of magnitude[5]. By relying on human reporting, there is also the possibility that the dataset we use might be biased towards more frequent reporting of large birds, or similar traits that influence detectability[22]. Furthermore, differences in sampling effort between regions may exacerbate such biases, if certain families are more common in sparsely sampled regions and are thus more less represented in WAHIS[14].

Partly because of biases in testing and reporting HPAI H5N1 outbreaks, we did not employ a presence/absence approach to modelling HPAI notifications and predicting susceptibility to disease in Australian species. Biases in testing and reporting, or lack of sufficient ornithological knowledge to identify specific species, mean we cannot assume that species absent from the WAHIS dataset of HPAI notifications truly never had cases of HPAI H5N1, and thus we cannot assume that HPAI is absent. However, our approach of using numbers of HPAI notifications still suffers from part of this bias and is likely to have influenced some of our predictions for Australian species. For example, Anhingidae (darters) are amongst families with the highest predicted notifications in Australia, but their non-Australian species are not currently represented in the WAHIS database. However, the American darter's (*Anhinga anhinga*) distribution includes regions severely impacted by the current panzootic, making it likely the species has encountered the virus but that it just has not been detected, tested and reported to WAHIS. The family's lack of representation in WAHIS means the model used the Anhingidae phylogenetic information, and its proximity to Sulidae and

Phalacrocoracidae (the latter of which is also underestimated in WAHIS[40]), to estimate a value between the two other families. The lack of Anhingidae representation in the WAHIS database, despite its probable interface with the virus, means the model may have over-estimated the susceptibility of Australasian darters to HPAI based on its relationship to Sulidae. An opposite scenario may also be possible and potentially detrimental: in some cases, our model may have falsely predicted a family as *not* susceptible to HPAI H5N1. This further highlights the importance of not relying on our predicted susceptibility in isolation, but also considering additional information. The wide host range of the current panzootic highlights that many species are capable of contracting the virus, however we need active monitoring of diverse species to confirm which families do and do not develop disease. However, lack of notifications and our assumptions of relative completeness in the WAHIS database impacts our predictions for Australian families susceptible to HPAI H5N1.

In our analysis, adding ecological traits like diet and habitat did not significantly improve the predictability of HPAI notifications above our null, phylogeny-only model. However, this does not mean those traits are not still important to consider when assessing virus incursion into new ranges, like Oceania. For example, traits like colony-breeding can amplify the risk to a species if the virus is able to spread rapidly through a large number of birds[18], but this also means there is a temporally-stratified risk to consider as colony-breeding is only a relevant trait at certain times of the year[21]. Australia hosts big breeding colonies of gannets, shearwaters, and other notable seabirds, which might expose them to the same colony-wide mass mortalities noted elsewhere[6,40,41]. Therefore, even if dense flocking behaviour was not a major predictor of HPAI notifications in our analysis, it is a trait worth bearing in mind when considering conservation impacts of potential HPAI H5N1 arrival in Australia. The same holds for diet and habitat traits, which were kept deliberately broad in our analysis. For example, the ecologies of geese and passerines were in this analysis occasionally grouped as ‘terrestrial omnivores’, but their distinct feeding ecologies and habitat movements can mean they will play very different roles in transmission of an HPAI H5N1 incursion into Australia. Similarly, analysis of the geospatial distribution of HPAI H5N1 has revealed that landscape characteristics can also influence risk[21], which will be crucial to consider when predicting potential incursion and spread in the Australian continent.

A strength of our phylogeny-based approach to model and predict HPAI notifications is that it likely captures similarity in immune architecture between closely related species, in addition to the ecological similarities it captures. However, there are notable exceptions to the expectation that closely related species share genomic similarities. Such differences in species' immune architecture may influence their final susceptibility to HPAI, and thus represents another aspect worth considering when predicting HPAI H5N1 susceptibility in new ranges[42]. For example, the Australian black swan (*Cygnus atratus*) is more vulnerable to HPAI than white swans and some geese[42], likely because it lacks receptors for viral pattern recognition and has a poor immune response to HPAI[43]. These differences set black swans apart even from closely related species, like the mute swan (*Cygnus olor*). Should similar deficiencies in immune system architecture exist for other Australian birds, it is possible the HPAI H5N1 susceptibility for some Australian birds is underestimated in our analysis. While our predictions of Australian species' susceptibility to disease from HPAI H5N1 can function as an important indicator of what is to come, expanded genomic and transcriptomic testing can further fine-tune such predictions.

Among other factors that can be important to consider when predicting HPAI H5N1 susceptibility in Australian birds is conservation status, where rampant disease spread may have a larger impact on more vulnerable populations[22]. In Australian species with highest predicted HPAI notifications (within the top 50 predicted HPAI H5N1 notifications), all but three are listed as Least Concern on the IUCN Red List status. Only the fairy tern (*Sternula nereis*), sooty tern (*Onychoprion fuscatus*), and the sarus crane (*Grus antigone*) are listed as Vulnerable. However, expanding this to species predicted to be moderately susceptible to HPAI (top 80 predicted disease notifications), there is one species listed as Endangered (red goshawk – *Erythrotriorchis radiatus*), two additional birds listed as Vulnerable (grey falcon – *Falco hypoleucos* and malleefowl – *Leipoa ocellata*), and one Near Threatened (letter-winged kite – *Elanus scriptus*). It is notable that most of these are birds of prey, suggesting that while HPAI H5N1 is primarily predicted to impact waterbirds, the notable conservation impacts of potential HPAI H5N1 incursion into Australia may focus on predators. The impact to predators might be similar to effects seen elsewhere[21], such as declining peregrine falcon (*Falco peregrinus*) populations in the Netherlands, where over 80% of tested dead birds were infected with HPAI H5N1[44]. Conservation vulnerability of predators to HPAI H5N1 also underscores the potential conservation concerns to mammalian predators[19], as has been noted in South American pinnipeds[45].

Conclusion

HPAI H5N1 has dramatically impacted wildlife in the wake of its spread across the world. While it has infected an unprecedented diversity of species, we found that a family-level phylogeny was sufficient to explain HPAI notifications in wild birds, potentially because ecological traits are often conserved across members of a family. Using this same phylogeny to predict HPAI notifications in Australian birds, where the virus has yet to spread, we are able to predict that Sulidae, Gruidae, Laridae, and Anatidae family members are likely to be most susceptible to disease from HPAI H5N1. Similarly, we are able to predict susceptibility to disease in Australian endemic families, such as the magpie goose (*Anseranas semipalmata*). Such predictions may provide important support for those undertaking planning for potential HPAI H5N1 incursion into Australia. Evaluating the accuracy of such predictions (and the method used to generate them) will only be possible once (or ‘if’) HPAI H5N1 does indeed reach Australian shores, and relies on continued and expanding monitoring efforts.

Acknowledgements

We wish to acknowledge the work testing and reporting HPAI outbreaks by scientists and community members worldwide, and WOAH WAHIS for storing all this data in their database and allowing us access. It should be noted that WOAH bears no responsibility for the integrity or accuracy of the data, including but not limited to any deletion, manipulation, or reformatting of data that may have occurred beyond its control. We would also like to thank our research partners at Wildlife Health Australia (WHA) for coordinating funding for this research, and the Department of Agriculture, Fisheries, and Forestry, for funding this work. Finally, we would like to thank our colleagues Libby Rumpff (Department of Climate Change, Energy, and the Environment and Water; DCCEEW), Mark Carey (DCCEEW), Simone Vitali (WHA), Tiggy Grillo (WHA), Claire Harrison (WHA), and Michelle Wille (University of Melbourne and the Peter Doherty Institute for Infection and Immunity) who read and provided feedback on the manuscript.

Author's contribution

Study conceptualisation and design: SR, TR, MK; data collation: SR, TR, MK; data analysis: SR with input from TR and MK; writing: SR with input from TR and MK.

Funding declaration

This project has financial support from the One Health Investigation Fund (administered by Wildlife Health Australia on behalf of the Commonwealth Department of Agriculture, Fisheries and Forestry).

Conflicts of interest/Competing interests

The authors declare no conflicts of interest.

References

1 Wille, M. & Waldenström, J. Weathering the storm of high pathogenicity avian influenza in waterbirds. *Waterbirds* **46**, 100-109, doi:https://doi.org/10.1675/063.046.0113 (2023).

2 CMS, F. C.-c. S. T. F. o. A. I. a. W. B. Scientific Task Force on Avian Influenza and Wild Birds statement on H5N1 high pathogenicity avian influenza in wild birds - Unprecedented conservation impacts and urgent needs., (2023.

3 Xie, R. *et al.* The episodic resurgence of highly pathogenic avian influenza H5 virus. *Nature* **622**, 810-817, doi:https://doi.org/10.1038/s41586-023-06631-2 (2023).

4 Wille, M. *et al.* Long-distance avian migrants fail to bring 2.3.4.4b HPAI H5N1 into Australia for a second year in a row. *Influenza and Other Respiratory Viruses* **18**, e13281, doi:https://doi.org/10.1111/irv.13281 (2024).

5 Klaassen, M. & Wille, M. The plight and role of wild birds in the current bird flu panzootic. *Nature Ecology & Evolution* **7**, 1541-1542, doi:https://doi.org/10.1038/s41559-023-02182-x (2023).

6 Lane, J. V. *et al.* High pathogenicity avian influenza (H5N1) in Northern Gannets (*Morus bassanus*): Global spread, clinical signs and demographic consequences. *Ibis* **166**, 633-650, doi:https://doi.org/10.1111/ibi.13275 (2024).

7 Alexandrou, O., Malakou, M. & Catsadorakis, G. The impact of avian influenza 2022 on Dalmatian pelicans was the worst ever wildlife disaster in Greece. *Oryx* **56**, 813-813, doi:https://doi.org/10.1017/S0030605322001041 (2022).

8 Kydyrmanov, A. *et al.* Mass mortality in terns and gulls associated with highly pathogenic avian influenza viruses in Caspian Sea, Kazakhstan. *Viruses* **16**, doi:https://doi.org/10.3390/v16111661 (2024).

9 James, J. *et al.* Clade 2.3.4.4b H5N1 high pathogenicity avian influenza virus (HPAIV) from the 2021/22 epizootic is highly duck adapted and poorly adapted to chickens. *Journal of General Virology* **104**, doi:https://doi.org/10.1099/jgv.0.001852 (2023).

10 Yang, Q. *et al.* Synchrony of bird migration with global dispersal of avian influenza reveals exposed bird orders. *Nature Communications* **15**, 1126, doi:https://doi.org/10.1038/s41467-024-45462-1 (2024).

11 Hill, N. J. *et al.* Ecological divergence of wild birds drives avian influenza spillover and global spread. *PLOS Pathogens* **18**, e1010062, doi:https://doi.org/10.1371/journal.ppat.1010062 (2022).

12 Damodaran, L., Jaeger, A. S. & Moncla, L. H. Ecology and spread of the North American H5N1 epizootic. *Nature* **649**, 432-441, doi:10.1038/s41586-025-09737-x (2026).

13 Trovão, N. S., Suchard, M. A., Baele, G., Gilbert, M. & Lemey, P. Bayesian Inference Reveals Host-Specific Contributions to the Epidemic Expansion of Influenza A H5N1. *Mol Biol Evol* **32**, 3264-3275, doi:10.1093/molbev/msv185 (2015).

14 Lambertucci, S. A., Santangeli, A. & Plaza, P. I. The threat of avian influenza H5N1 looms over global biodiversity. *Nature Reviews Biodiversity* **1**, 7-9, doi:https://doi.org/10.1038/s44358-024-00008-7 (2025).

15 Wille, M. *et al.* Strong host phylogenetic and ecological effects on host competency for avian influenza in Australian wild birds. *Proceedings of the Royal*

Society B: Biological Sciences **290**, 20222237, doi:https://doi.org/10.1098/rspb.2022.2237 (2023).

16 European Food Safety Authority, E. C. f. D. P. *et al.* Avian influenza overview June–September 2024. *EFSA Journal* **22**, e9057, doi:https://doi.org/10.2903/j.efsa.2024.9057 (2024).

17 van Dijk, J. G. B., Verhagen, J. H., Wille, M. & Waldenström, J. Host and virus ecology as determinants of influenza A virus transmission in wild birds. *Current Opinion in Virology* **28**, 26-36, doi:https://doi.org/10.1016/j.coviro.2017.10.006 (2018).

18 McPhail, G. M. *et al.* Geographic, ecological, and temporal patterns of seabird mortality during the 2022 HPAI H5N1 outbreak on the island of Newfoundland. *Canadian Journal of Zoology* **103**, 1-12, doi:https://doi.org/10.1139/cjz-2024-0012 (2024).

19 Tammiranta, N. *et al.* Highly pathogenic avian influenza A (H5N1) virus infections in wild carnivores connected to mass mortalities of pheasants in Finland. *Infection, Genetics and Evolution* **111**, 105423, doi:https://doi.org/10.1016/j.meegid.2023.105423 (2023).

20 Gorta, S. B. Z., Berryman, A. J., Kingsford, R. T., Klaassen, M. & Clarke, R. H. Kleptoparasitism in seabirds—A potential pathway for global avian influenza virus spread. *Conservation Letters* **n/a**, e13052, doi:https://doi.org/10.1111/conl.13052 (2024).

21 Hayes, S. *et al.* Ecology and environment predict spatially stratified risk of H5 highly pathogenic avian influenza clade 2.3.4.4b in wild birds across Europe. *Scientific Reports* **16**, 997, doi:10.1038/s41598-025-30651-9 (2025).

22 Pearce-Higgins, J. W. *et al.* Assessing the vulnerability of wild bird populations to high pathogenicity avian influenza. *Bird Study* **72**, 5-19, doi:10.1080/00063657.2025.2494164 (2025).

23 WOAH [Word Organisation for Animal Health]. Terrestrial Animal Health Code. (2025<https://www.woah.org/en/what-we-do/standards/codes-and-manuals/>).

24 Arel-Bundock, V., Enevoldsen, N. & Yetman, C. countrycode: An R package to convert country names and country codes. *Journal of Open Source Software* **3**, 848, doi:https://doi.org/10.21105/joss.00848 (2018).

25 Tobias, J. A. *et al.* AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* **25**, 581-597, doi:https://doi.org/10.1111/ele.13898 (2022).

26 Billerman, M. S., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. (Cornell Labratory of Ornithology, Ithaca, NY, USA, 2022).

27 R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, 2023).

28 Bürkner, P.-C. brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1-28, doi:https://doi.org/10.18637/jss.v080.i01 (2017).

29 Kuhl, H. *et al.* An unbiased molecular approach using 3'-UTRs resolves the avian family-level tree of life. *Molecular Biology and Evolution* **38**, 108-127, doi:https://doi.org/10.1093/molbev/msaa191 (2021).

30 Louca, S. & Doebeli, M. Efficient comparative phylogenetics on large trees. *Bioinformatics* **34**, 1053-1055, doi:https://doi.org/10.1093/bioinformatics/btx701 (2018).

31 Yu, G., Smith, D. K., Zhu, H., Guan, Y. & Lam, T. T.-Y. ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* **8**, 28-36, doi:https://doi.org/10.1111/2041-210X.12628 (2017).

32 Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag New York, 2016).

33 rredlist: 'IUCN' Red List Client (R package version 0.7.1, 2022).

34 Sivula, T., Magnusson, M., Matamoros, A. A. & Vehtari, A. Uncertainty in Bayesian leave-one-out cross-validation based model comparison. *arXiv*, doi:https://doi.org/10.48550/arXiv.2008.10296 (2023).

35 Norman, D., MacLeod-Nolan, C. & Berthelsen, U. M. Near-absence of high pathogenicity avian influenza (HPAI) in Little Terns Sternula albifrons across 13 European countries. *Bird Study* **71**, 347-352, doi:10.1080/00063657.2025.2450551 (2024).

36 Rayment, K. M. *et al.* Exposure and survival of wild raptors during the 2022–2023 highly pathogenic influenza a virus outbreak. *Scientific Reports* **15**, 6574, doi:https://doi.org/10.1038/s41598-025-90806-6 (2025).

37 McLaughlin, A. *et al.* Examining avian influenza virus exposure in seabirds of the northwest Atlantic in 2022 and 2023 via antibodies in eggs. *Conservation Physiology* **13**, coaf010, doi:10.1093/conphys/coaf010 (2025).

38 Signore, A. V. *et al.* Spatiotemporal reconstruction of the North American A(H5N1) outbreak reveals successive lineage replacements by descendant reassortants. *Science Advances* **11**, eadu4909, doi:10.1126/sciadv.adu4909.

39 Kingsford, R. T., Roshier, D. A. & Porter, J. L. Australian waterbirds – time and space travellers in dynamic desert landscapes. *Marine & Freshwater Research* **61**, 875-884, doi:10.1071/MF09088 (2010).

40 Kuiken, T. *et al.* Emergence, spread, and impact of high pathogenicity avian influenza H5 in wild birds and mammals of South America and Antarctica, October 2022 to March 2024. *EcoEvoRxiv*, doi:https://doi.org/10.32942/X2P35R (2025).

41 Tremlett, C. J., Cleasby, I. R., Bolton, M. & Wilson, L. J. Declines in UK breeding populations of seabird species of conservation concern following the outbreak of high pathogenicity avian influenza (HPAI) in 2021–2022. *Bird Study*, 1-18, doi:https://doi.org/10.1080/00063657.2024.2438641 (2025).

42 Brown, J. D., Stallknecht, D. E. & Swayne, D. E. Experimental infection of swans and geese with highly pathogenic avian influenza virus (H5N1) of Asian lineage. *Emerging Infectious Diseases* **14**, 136-142, doi:https://doi.org/10.3201/eid1401.070740 (2008).

43 Karawita, A. C. *et al.* The swan genome and transcriptome, it is not all black and white. *Genome Biology* **24**, 13, doi:10.1186/s13059-022-02838-0 (2023).

44 Caliendo, V. *et al.* Highly pathogenic avian influenza contributes to the population decline of the Peregrine Falcon *(Falco peregrinus*) in the Netherlands. *Viruses* **17**, doi:https://doi.org/10.3390/v17010024 (2025).

45 Campagna, C. *et al*. Catastrophic mortality of southern elephant seals caused by H5N1 avian influenza. *Marine Mammal Science* **40**, 322-325, doi:https://doi.org/10.1111/mms.13101 (2024).