Predicting high pathogenicity avian influenza H5N1 susceptibility in wild birds

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

[1]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 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 wreaked havoc on poultry and wildlife for decades, causing tremendous 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) and causing large scale mortalities in poultry and wild birds, increasingly also spilling 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[10,11]. 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 paramount 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[5,12]. Presence of LPAI, from which HPAI evolves, has a strong phylogenetic signal in wild birds[13], 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[13]. 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 LPAI to the current HPAI H5N1 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 interaction with the transmission pathway. Avian influenza transmission occurs through 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[14,15]. Colony breeding, and specific colony traits such as distance between nests, have also been implicated in HPAI H5N1 spread[14,16]. Based on infection patterns in predatory birds and mammals, HPAI H5N1 is also capable of spreading via consumption of infected birds[1,17] and potentially via kleptoparasitism[18]. These distinct transmission pathways present particularly "risky ecologies" for birds to have, in terms of likelihood of 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. However, empirical testing of these potentially "risky ecologies" across known cases of H5N1 are generally restricted to certain regions (e.g.[16,19]), 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 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 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. 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 susceptibility in Australian birds, as the last remaining continent not yet affected by 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. 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. While underreporting of outbreaks is likely an issue with this database[5], it still provides a minimum indication of HPAI notifications because each notification may represent a single bird or multiple birds from a single species. The database was accessed on 06/01/2025 and filtered to only include notifications of outbreaks reported in wild birds of known species since October 2021. In 99% of the cases, the serotype of the HPAI notification was evaluated and established to be HPAI H5. We therefore assume that the majority (if not all) notifications used in our study relate to HPAI H5N1. 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.

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 H5N1 notifications in wild birds. Initial ecological categorisations of habitat and trophic niche were obtained from Avonet[20]. 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[21], and broadened the groupings. We thus had three categories for habitat: Terrestrial, Freshwater, and Coastal/Marine, and three categories for diet: Predators (including scavengers, vertebrate and invertebrate predators), Plant-based diets (including aquatic and terrestrial plant material), and Omnivores (including any species that were both predators and plant-based feeders). 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[21]. For a full list of species and our ultimate ecological categorisation for these species, see Supporting Information Table S1.

To predict HPAI 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[22].

To model HPAI H5N1notifications in birds, we used a phylogenetic generalised linear mixed model (GLMM) in the 'brms' package[23]. We used a Poisson distribution of the number of HPAI notifications, modelled against the phylogeny. For the phylogeny, we used the family-level phylogeny from[24]. 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 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 = 3 categories), and whether the species is known to congregate (Y/N). We fitted three models that had one single ecological predictor (habitat, diet, or congregation), and then an additional model that included all 3 ecological predictors. We evaluated model fit of these against the null, 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 it arrives in Australia, based on patterns of HPAI H5N1 notifications elsewhere in the world. We used the HPAI notification data to predict numbers of HPAI H5N1 notifications in Australian birds, and use this as our metric of predicted susceptibility to HPAI H5N1. Most (~98%) of HPAI notifications in the WAHIS database since October 2021 report deaths for species that have outbreak notifications, which means that our predicted susceptibility to infection 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[24], thus resulting in a phylogeny with the families in the WAHIS database and the Australian families. Using the 'castor' package[25], we predicted HPAI H5N1 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 H5N1 notifications for Australian bird families, which we interpreted as their predicted susceptibility to HPAI H5N1.

Plots were made using 'ggtree'[26] and 'ggplot2'[27]. Lastly, we extracted IUCN Redlist status for Australian species using the 'rredlist' package[28], to ascertain the conservation status of any species predicted to be highly susceptible to HPAI H5N1 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 H5N1 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 H5N1 in wild birds since October 2021 using the phylogeny-only model, we found a statistically significant phylogenetic signal (Pagel's λ: 0.54, 95% CI: 0.04 – 0.84). There were predominantly high numbers of HPAI H5N1 notifications amongst Sulidae (gannets and boobies), Laridae (gulls, terns, and noddies), and Anatidae (ducks, geese, and swans). To a lesser extent, other seabirds (like Pelecanidae [pelicans] and Alcidae [auks]), crows and ravens (Corvidae), and birds of prey (like Falconidae and Accipitridae) also had higher numbers of HPAI H5N1 notifications (Figure 1).

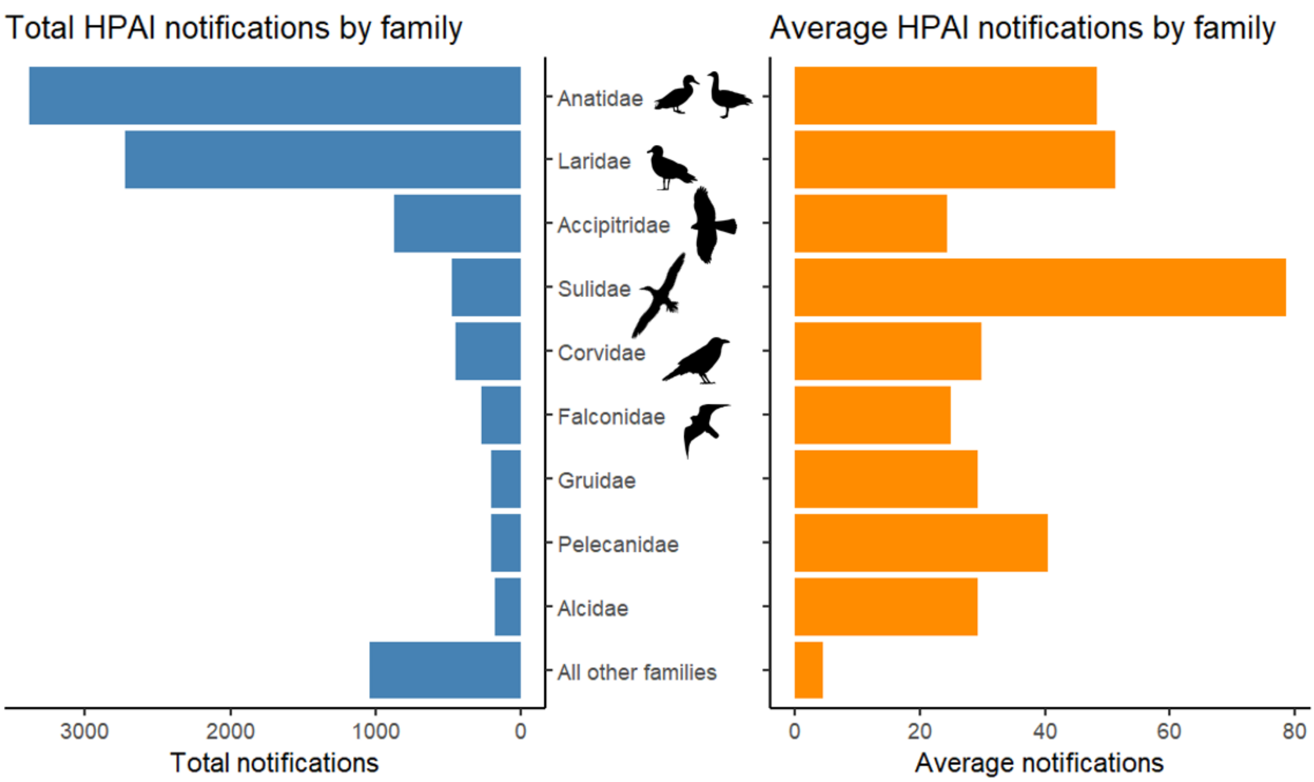

Figure 1. HPAI H5N1 notifications in wild birds 2021 – 2024. The left panel shows total HPAI H5N1 notifications made to WOAH WAHIS per family, while the right panel shows average HPAI H5N1 notifications per family. A few key families are highlighted by inclusion of bird icons from phylopic.org, going down from the top: Anatidae, Laridae, Accipitridae, Sulidae, Corvidae, and Falconidae.

Using leave-one-out (LOO) cross validation, we compared the fit of this null, 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. All four of these models included the phylogeny. 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;[29]). Therefore, we present results for the simpler, phylogeny-only model.

When predicting Australian species' HPAI H5N1 susceptibility (defined as their predicted HPAI H5N1 notifications), the predominant groupings of predicted notifications were similar to that of the training model (Figure 2). The highest predicted HPAI H5N1 susceptibility was predicted for Australian Sulidae (gannets and boobies), followed by Anhingidae (darters), Laridae (gulls, terns and noddies), and Anatidae (ducks, geese, and swans). Based on global HPAI H5N1 notification data since 2021 and the family-level phylogeny, the model predicted 79 HPAI H5N1 notifications in Sulidae family members, followed by 54 in Anhingidae, 51 in Laridae, and 48 in Anatidae family members. Other Australian bird families, like Pelecanidae (pelicans), Corvidae (crows and ravens), and Falconidae (falcons, hobbies, and kestrels), were also predicted to be susceptible. Furthermore, some families endemic to Australia, such as Anseranatidae (containing the magpie goose – *Anseranas semipalmata*), were predicted to be moderately susceptible to HPAI H5N1 with a predicted 27 notifications. Predicted HPAI H5N1 notifications for all Australian bird families in our list are reported in Supporting Information Table S3.

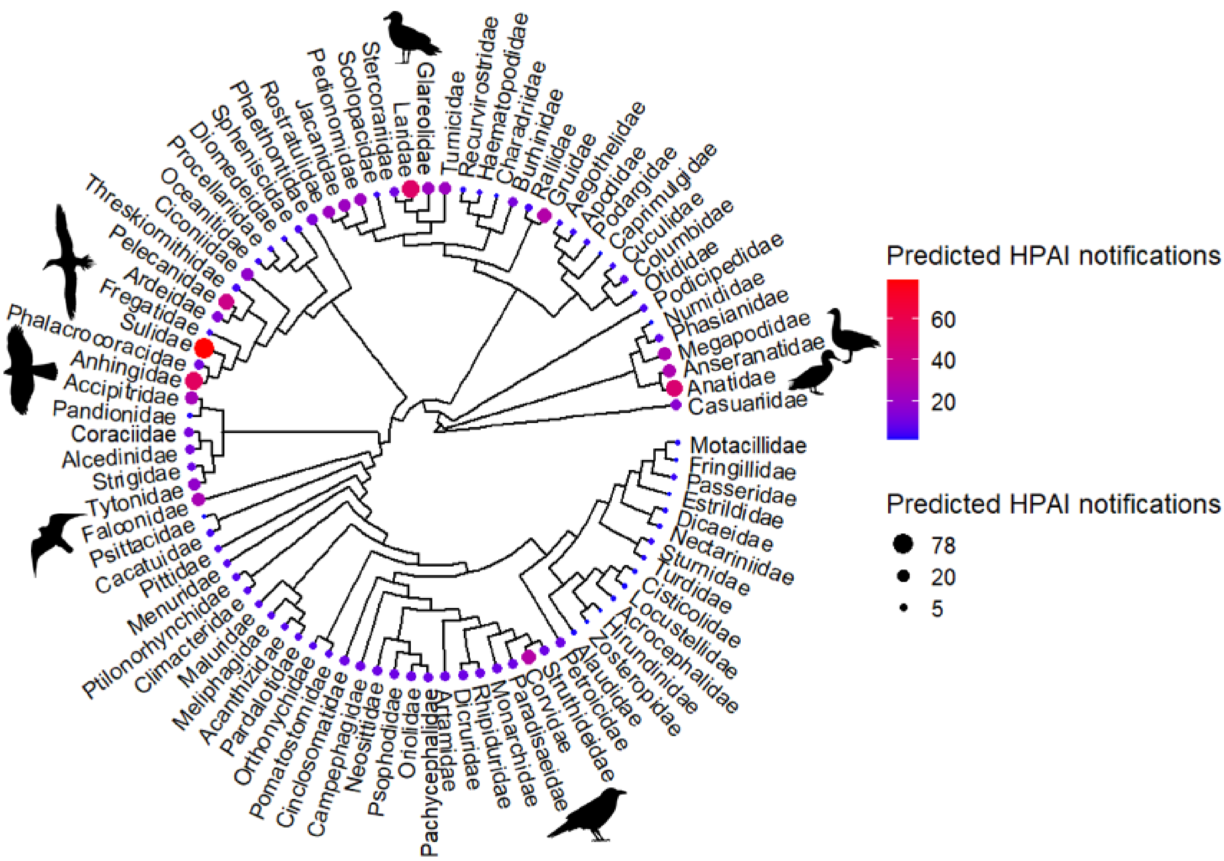

Figure 2. Predicted HPAI H5N1 susceptibility for Australian bird families. Each tip denotes a family, with the size and colour of the tip representing the predicted number

of HPAI H5N1 notifications. A few key families are highlighted by inclusion of bird icons from phylopic.org, going clockwise from the top: Laridae, 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 H5N1 notifications as a function of ecology and family-level phylogeny, finding that family-level phylogeny best explains number of HPAI H5N1 notifications. The importance of phylogeny in explaining avian influenza prevalence has been previously noted for low pathogenicity viruses[13], which we now expand for HPAI H5N1. Furthermore, we use phylogeny to predict HPAI H5N1 notifications in Australian birds (including for Australian endemic birds), as a metric of susceptibility to HPAI H5N1 infection and resulting disease once 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 HPAI H5N1 in Australia, likely due to their aquatic lifestyle. Conversely, we hypothesized terrestrial birds to have lower HPAI H5N1 notifications due to largely avoiding contact with HPAI virus contaminated water, but many birds of prey (which have high HPAI H5N1 notifications) are terrestrial predators. This specific interaction between diet and habitat may be important in predicting HPAI H5N1 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 H5N1 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 H5N1 notifications for the Australasian wood duck (*Chenonetta jubata*), despite its ecology differing from other ducks (it is an exclusively grazing duck, while many others engage in filter feeding and dabbling) and its previous identification as an outlier in having low LPAI virus and seroprevalence[13]. 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[30]. 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 H5N1 notification for a taxonomic family (where high numbers of predicted HPAI H5N1 notifications is interpreted as high susceptibility; with 79 HPAI H5N1 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 (~98%) species with notifications also have reported deaths from HPAI. This means that our predicted HPAI H5N1 susceptibility 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 carry the virus and survive 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[31], and HPAI antibodies in seabird eggs were higher in common eiders compared to other seabird species (such as gannets, which suffered HPAI-related mass mortality events[32]). In the current HPAI panzootic, recent research has shown that the host dynamics of H5N1 differs between virus genotypes[33], showcasing the wide range of birds capable of contributing to the spread of HPAI and that the reservoir community can change rapidly. 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.

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 H5N1 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 H5N1 notifications across a family (rather than just the total), we avoid some of the exaggerated total HPAI H5N1 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 H5N1 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[19]. 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[12].

Partly because of biases in testing and reporting HPAI H5N1 outbreaks, we did not employ a presence/absence approach to modelling HPAI H5N1 notifications and predicting susceptibility in Australian species. Because of testing and reporting bias, we cannot assume that species absent from the WAHIS dataset of HPAI H5N1 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 H5N1 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[34]), 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 H5N1 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 all species are capable of contracting the virus. 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 H5N1 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[16]. 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[6,34,35]. Indeed, in our phylogeny-based predictions of HPAI H5N1 notifications in Australian birds, half of the top 50 birds are colony breeders. Therefore, even if dense flocking behaviour was not a major predictor of HPAI H5N1 notifications in our analysis, it is a trait worth bearing in mind when considering conservation impacts of HPAI H5N1 upon arrival in Australia.

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[36]. For example, the Australian black swan (*Cygnus atratus*) is more vulnerable to HPAI than white swans and some geese[36], likely because it lacks receptors for viral pattern recognition and has a poor immune response to HPAI[37]. 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 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[19]. In Australian species with highest predicted HPAI H5N1 notifications (within the top 50 predicted HPAI H5N1 notifications), all but two are listed as Least Concern on the IUCN Red List status. Only the fairy tern (*Sternula nereis*) and the sarus crane (*Grus antigone*) are listed as Vulnerable. However, expanding this to species predicted to be moderately susceptible to HPAI H5N1 (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 HPAI H5N1 incursion into Australia may focus on predators. The impact to predators might be similar to effects seen elsewhere, such as declining peregrine falcon (*Falco peregrinus*) populations in the Netherlands, where over 80% of tested dead birds were infected with HPAI H5N1[38]. Conservation vulnerability of predators to HPAI H5N1 also underscores the potential conservation concerns to mammalian predators[17], as has been noted in South American pinnipeds[39].

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 H5N1 notifications in wild birds, potentially because ecological traits are often conserved across members of a family. Using this same phylogeny to predict HPAI H5N1 notifications in Australian birds, where the virus has yet to spread, we are able to predict that Sulidae, Laridae, and Anatidae family members are likely to be most susceptible to HPAI H5N1. Similarly, we are able to predict susceptibility in Australian endemic families, such as the magpie geese (*Anseranas semipalmata*). Such predictions may provide important support for those undertaking planning for HPAI H5N1 incursion into Australia. Evaluating the accuracy of such predictions (and the method used to generate them) will only be possible once HPAI H5N1 does indeed reach Australian shores, and relies on continued and expanding monitoring efforts.

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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.

Availability of data and material

Data and code are available via figshare (private link for review: https://figshare.com/s/4c3cf05991ac9b50d19e) and will be made public upon acceptance

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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 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).

13 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).

14 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).

15 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).

16 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).

17 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).

18 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).

19 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).

20 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).

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

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

23 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).

24 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).

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

26 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).

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

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

29 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).

30 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).

31 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).
32 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).
33 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.
34 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).
35 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).
36 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).
37 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).
38 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).
39 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).