HPAI virus transmission is shaped by inter-specific social network structure.

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Abstract: The emergence of zoonotic and epizootic disease from communities of wild animals is a recurrent threat to human and animal health, to food and economic security. This is particularly true for disease systems that involve many interacting species, where the varied ecological and behavioural diversity of those species interact, driving complex pathways of transmission, and where sampling many species across time and space is difficult. As a consequence, surveillance of disease across communities of wild animals is largely reliant on responsive, rather than preventative, sampling after an outbreak event. Here, we inferred social networks of wild birds using five years of bird survey data from a county in Northern England. We mapped 8,162 links between 159 species, and combined this with Highly Pathogenic Avian Influenza virus (HPAIV) genomic similarity measures from 35 host species, measured over 388 sequences. Inter-specific social network position predicted similarity between viral genomes, consistent with HPAIV transmission between species that co-occur in the wild. Our results have important applications for surveillance and prioritization of zoonotic and epizootic disease, and provide an empirical basis for future theoretical and species trait-based evaluation of pathogen spread among ecological communities.

Introduction: The repeated emergence of zoonotic and epizootic diseases of pandemic potential from communities of wild animals is a recurrent threat to human and animal health (Kruse, Kirkemo, and Handeland 2004; Kuiken et al. 2005; Karesh et al. 2012; Holmes 2022; World Health Organization 2024), with far-reaching consequences for global economic and food security (Clemmons, Alfson, and Dutton III 2021; Bernstein et al. 2022). For example, Avian Influenza viruses (AIVs), SARS-CoV-2, Ebola virus, Herpes viruses, Marburg virus, MERS-CoV and West Nile virus all originate from communities of wild animals with little detection prior to outbreaks in humans or livestock (Jones et al 2008; Carlson et al. 2022). However, in (non-human) animal communities, patterns of disease transmission are highly variable, and cannot be solely explained by pathogen virulence. Instead, just as human mobility and interaction shapes the trajectory of an epidemic, (Firth et al. 2020; Kraemer et al. 2020; Kostandova et al. 2024, 2025), animal social network structure, shaped by host ecology and the social and physical environment, must also influence disease propagation through communities of wild animals.

Wild animal social systems, involving many interacting individuals, are complex and dynamic, shaped by the demography and varied behavioural preferences of their constituents (Kulahci and Quinn 2019; Albery et al. 2022; Beck, Sheldon, and Firth 2023; Dunning et al. 2023; Schroeder et al. 2024), and the physical and social environments within which they exist (Firth, Sheldon, and Farine 2016; Firth, Sheldon, and Brent 2017; Motes-Rodrigo et al. 2025). This complexity is magnified in inter-specific, or multi-host systems, where many species with a broad diversity of behavioral traits and spatial preferences, interact (Bansal, Grenfell, and Meyers 2007; Buhnerkempe et al. 2015; Sah et al. 2017; Sah, Mann, and Bansal 2018; Farine, Garroway and Sheldon 2020; Hillemann et al. 2020; Collier et al. 2022). It is this inherent complexity that drives network structure and, in the context of non-vector-borne disease, provides the network links through which disease may spread (Bansal, Grenfell, and Meyers 2007; Wolinska and King 2009; Sah, Mann, and Bansal 2018; King, Hall, and Wolinska 2023; Prosser et al. 2023). For example, during the H5N1 2.3.4.4b highly pathogenic avian influenza (HPAI) outbreak that affected seabirds in Western Europe in the summer of 2021, the presence of disease in otherwise isolated

nesting colonies of Northern Gannet *Morus bassanus* prompted a short-term increase in between-colony connectivity, as birds abandoned infected breeding sites, shaping the structure of the social network and driving further spread through seabirds (Jeglinski et al. 2024). This host expansion had devastating consequences for the conservation of affected wild birds (Banyard et al. 2022; Falchieri et al. 2022; Pohlmann et al. 2023; Macgregor et al. 2024; Tremlett et al. 2025), but also drove HPAI spread into new continents (Letsholo et al. 2022; Stokstad 2022; Kandeil et al. 2023; Andrew et al. 2024; Bennison et al. 2024) and novel systems like domestic and wild mammals (Burrough et al. 2024; Plaza et al. 2024; Sah et al. 2024; Uhart et al. 2024) including humans (Li et al. 2019; Sidik 2023).

It is perhaps because of this complexity, that research into animal disease systems has tended to focus on the role of specific traits (Garamszegi and Møller 2007; Luis et al. 2015; Tian et al. 2015; Olival et al. 2017; Albery et al. 2020, 2021; Pearce-Higgins et al. 2023; Yin et al. 2023; Vickers et al. 2024) and/or environmental components (Keesing et al. 2010; Carlson et al. 2022; King, Hall, and Wolinska 2023; Prosser et al. 2023; Desvars-Larrive et al. 2024), rather than the structure of the global social system. However, most traits (e.g. shared habitat, dietary preference, or migratory phenology) and environmental conditions influence transmission by shaping community network structures – forcing potential hosts together or driving them apart. This spatial and temporal clustering either facilitates or constrains pathogen transmission through social links

Understanding first the pattern of disease spread through multi-host networks, and then the traits and conditions that shape those networks, are both important knowledge gaps to informing preventative surveillance and prioritization of zoonotic and epizootic disease systems (Luis et al. 2015; Marí Saéz et al. 2015; Olival et al. 2017; Bonneaud and Longdon 2020, Desvars-Larrive et al. 2024; Webby and Uyeki 2024). Both have been challenging to test empirically and perhaps as a consequence evaluation of multi-host network disease dynamics has been reliant on theoretical models (Sah et al. 2017; Albery et al. 2020, 2021; McDuie et al. 2024; Ryding, Ross, and Klaassen 2025). There is therefore a pressing need for new predictive approaches to identify the species and

pathways that drive zoonotic and epizootic disease spread, in order to inform risk-based policy interventions. To test the hypothesis that social proximity in multi-species networks of wild animals predicts disease transmission, something that although is often assumed, has been very difficult to demonstrate in a wild system, we evaluated the relationship between wetland bird community structure and genomic relatedness between highly pathogenic avian influenza (HPAI) viruses sampled from species found in those communities. HPAIs represent a disease system with a broad geographic and host taxonomic span (Lupiani and Reddy 2009; Klaassen and Wille 2023; Webby and Uyeki 2024) with recurrent diseases of wildfowl and waterbirds wildfowl (Pohlmann et al. 2022; Atkinson and Baillie 2024) and frequent incursion into poultry (Lupiani and Reddy 2009; Lycett, Duchatel, and Digard 2019; Gao 2014; Blagodatski et al. 2021).

Recent access to large repositories of citizen-science data on wild animal distributions (Sullivan et al. 2009; Albery et al. 2020; Macgregor et al. 2024; Vickers et al. 2024), alongside sampling and sequencing of viruses circulating within these communities (Byrne et al. 2023; Gamża et al. 2024) now provides an opportunity to study the effect of social network structure on the spread of zoonotic and epizootic disease in wild animals. To demonstrate this, we used HPAI as a study system - HPAI represents a serious threat to public health (World Health Organization 2024; UK Health Security Agency 2025), with trans-boundary transmission between hundreds of interacting hosts (Klaassen and Wille 2023), and via multiple channels of transmission (Malik et al. 2021; Sun et al. 2018; Reid et al. 2024). But, up to now, access to host ecology data and sampling for HPAI in the environment have been major constraints to landscape-scale predictive modelling (Kruse, Kirkemo, and Handeland 2004; Kuiken et al. 2005),

Although several studies have described inter-specific HPAI transmission within communities of wild birds (Boulinier 2023; Coffey and Verspoor 2025), and in some cases in response to disease within the network (Jeglinski et al. 2024; but also see Teitelbaum et al. 2023), or aligned phenology of wild bird behaviours with outbreaks in poultry (Tian et al. 2015; Vickers et al. 2024; Gamża et al. 2024; Shemmings-Payne et al. 2024), at present, HPAI surveillance, and predictive modelling, is limited by reactive (i.e. *post* disease emergence) virus sample collection and processing availability, and

taxonomic biases in existing sampling data (Wade et al. 2022; Atkinson et al. 2025, but also see, Wannigama et al. 2025). Social networks have been applied to simpler, direct transmission (Côté and Poulinb 1995; Gómez, Nunn, and Verdú 2013), and single species systems (Wilson-Aggarwal et al. 2019; Proboste et al. 2024), including humans (Klovdahl 1985; Firth et al. 2020), but not yet in complex transmission systems of wild animals.

We combined social network analysis with a viral phylodynamic and Bayesian generalized (non-)linear multilevel models to test the relationship between co-occurrence of wild birds in the landscape and genetic distance between HPAI viral genomes. We predict that social links will correlate with HPAI viral genome similarity, a proxy for transmission, in a multi-species network of wild birds, at the landscape scale.

Methods: To test the hypothesis that social proximity predicts more similar virial genetic distances across multi-species networks of wild birds, we combined social network analysis with phylodynamic and Bayesian mixed modelling approaches. We tested if our results differed from the expected network, without social structure, by running a series of permutations that mirrored our observed data models.

Survey effort and Networks: To build species co-occurrence networks, we accessed five years of data from the British Trust for Ornithology Wetland Bird Survey (WeBS), 2018 - 2022 for two overlapping regions of East Yorkshire, UK, each defined by a 50km circular buffer around two recurrent HPAI outbreak sites. Each year represented a number of sampling events (surveys) within the non-breeding season (October to March; for more information of WeBS survey methods, see Woodward et al. 2024).

From these networks we extracted two established dyadic (pairwise - between two species) measures of association from our social networks. To measure the extent to which two species co-occur in the landscape, and therefore, may be expected to share virus more easily, we used pairwise edge weight, the absolute frequency of co-occurrence in the network; Then, to capture the extent to which a species pair are associated in space and time, accounting for absolute co-occurrence relative to the opportunity for co-occurrence, we also used the Simple Ratio Index (SRI; see Farine and Whitehead 2015), that measures between 0 (no over-lap between a species) and 1 (where one species is recorded so is the other, without exception). Although both measure interaction between species, pairwise weight and SRI represent different aspects of interaction in the landscape. Where pairwise weight is the absolute frequency of co-occurrence and a high value denotes stronger co-occurrence in the landscape, a higher SRI value represents stronger relative association, regardless of abundance. For example, in our WeBS data, the highest SRI are between relatively scarce species that share a habitat niche, for example Dipper *Cinclus cinclus* and Grey Wagtail *Motacilla cinerea* that both favor fast flowing upland streams. Although they are both rare in the landscape, they are almost always recorded at the same sites. Finally, we restricted the network used in our models to only include the species also present in

the viral phylodynamic study (see below), while weights and SRI measures were calculated and carried over from the global social network.

Network similarity: We tested the assumption that out networks are comparable between years, that is that the dyads that make up the general network structure were similar across our five years of data collection. We did this using two measures designed to compare non-uniform networks, in this case, with variation in the species recorded -the network actors (nodes)- between years: 1) Jaccard similarity describes the proportion of shared dyads between two networks, regardless of weight; and, 2) a Spearman rank correlation test to measure similarity of dyadic edge weights between species pairs present in both networks. In both cases 1 denotes identical network structure, and 0 denotes no relationship.

Viral genetic similarity: We accessed 715 viral full genome sequences of H5N1 viruses collected in Great Britain, initially from 59 host species from the Global Initiative on Sharing All Influenza Data (GISAID), a global repository including Influenza genome data. To define genetic distance between viral genome sequences, we classified them by reassortment profile (see Gamża et al. 2024). We aligned the sequences using MAFFT v7.511 (Katoh and Standley 2013), trimmed them to coding regions, removed insertions present in fewer than 10% of sequences and rejected sequences with nucleotide coverage lower than 80% for all segments. We identified clusters for each of the eight gene segments using nearest-neighbor hierarchical clustering of nucleotide distances in the bioseq package in R (Keck and Mahon 2020; R Core Team 2023). We used a 0.5% distance threshold for the Polymerase Basic (PB)1, PB2, and Polymerase Acidic gene segments, and 1% for all others. We aligned each sequence with host information, after filtering out mammals, domestic birds and taxonomically vague entries (none of which are recorded as part of WeBS surveys), as well as non- H5N1 strains (H5N5 and H5N8). We recorded the date associated with each sampling event and a location, provided by the Animal and Plant Health Agency (APHA). We compared each sequence with all others in the database to quantify a genetic distance between pairwise viral genomes using the Tamura and Nei 1993 model (Tamura & Nei, 1993) using the APE package for R (Emmanuel Paradis, 2024)) that calculates genetic

distance as a proportion that differ between each pair of sequence, accounting for difference in rates for both kinds of transition and transversion., as well as measures of geometric (space between sampling events) and temporal (time between sampling events) distance. For more details on how these data were generated see Gamża et al. (2024). Finally, we further filtered these data to only include species pairs also present in at least one of our five social networks, leaving 763 pairwise samples between 19 wild host species.

Data structure: To test our predictions that high between-species co-occurrence, or greater association between a species pair, should result in a greater chance of viral transmission, we built and extracted edge-based centrality metrics from five years of BTO WeBS data and modeled these against similarity of host viral genomes (genetic distance). We used smaller genetic distance (more similar) between viral sequences as a proxy for transmission, yet, because there are relatively few viral samples taken from relatively few wild bird hosts (relative to the number in the social networks) our models only contained species present in both data-sets. We used the maximum genetic distance between host samples as the response variables, and controlled for the space and time-elapsed between sampling as well as the contribution of species within our dyads as individuals in our fixed effects, in all of our models.

Model fit: To test the relationship between wild bird social network structure and genetic distance between HPAI viruses, and to accommodate multi-membership sampling in our species dyads, we ran a series of Generalized Linear Mixed Models (GLMMs) using Bayesian Markov Chain Monte Carlo (MCMC) simulations with the Hamiltonian Monte Carlo (HMC) and No-U-Turn Sampler (NUTS) algorithms in the brms package (Bürkner 2017). All models used the maximum genetic distance (least similar) between pairwise viral genomes, a conservative proxy for transmission between hosts, as the response variable. Otherwise, our models only differed only by the first predictor (fixed effect) variable, which was either pairwise weight or SRI. For all models, we used weakly informative priors, and ran each over 4 chains of 4,000 iterations, with a warm-up of 1,000 iterations and a thinning interval of 1. We used Effective Sample Sizes (ESS) of >5000 in the posterior and tail distributions to maintain sampling efficiency and

a scale reduction factor (Ř) values of 1 to ensure convergence. We also manually checked posterior trace plots to ensure model mixing. The fixed effects were considered statistically significant when the 95% credible interval (CI) excluded zero.

Pairwise weight: We modeled pairwise weight, the mean of geometric distance between viral pairwise sample locations and the mean of pairwise temporal distance (time elapsed between sampling events) as fixed effects. We z-transformed all fixed effects to better align scales between other variables in the model. We used the mean (rather than the max) of geometric- and temporal distance to account for wide variation in sampling and to reduce marginal collinearity. Because most species appeared across many dyads, we accounted for species specific effects on genetic distance independently of their dyad (i.e. species A + species B, rather than speciesAB) by including species A and species B as a linked ‘multi-membership’ variable inside our random effects. This approach also avoided over-dispersion.

SRI: We repeated the first model, using the same model structure but with SRI, instead of pairwise weight, as a fixed effect. We used the log-odds (using a logit link function) of SRI to better accommodate a linear relationship between SRI and other predictors in the model.

Permutations: In order to test that our results differed from the expected distribution without social structure in the network, we repeated our models with a series of network permutations. We did this by ‘re-wiring’ the observed network, shuffling the edges between species pairs while maintaining the degree distribution for each species node (Csardi and Nepusz 2006). We rewired networks 1000 times within years, before combining them into a global network within each permutation cycle. Edges were rewired between species nodes, breaking the community structure of the observed network, but, because some species are much more frequent in our data -and therefore our networks have some strong ties- we sampled edges from the empirical distribution of edge weights (Farine 2017). This controlled for the chance that some effects are the result of some species having more interactions over all, rather than who those interactions were with. We maintained the structure of our original models, but because we were only interested in effect sizes we reduced the number of iterations and the

warm up by half (from 4000 to 2000, and 1000 to 500, respectively) and ran the permutation over 100 cycles. We inferred significance, that the effect of social structure on genetic distance in our observed models was stronger than expected under a system of random mixing, where our observed credible intervals fell outside of the 95% confidence intervals of the permuted estimate.

Results:

Data Structure:

Our global network contained 8,035 dyads between 159 species nodes. We constructed this network from five years of Wetland Bird Surbey data from the BTO, summarized in Table 1A. thew structure of these networks were consistent over time, measured in their species composition, and the relative edge weights between species pairs, given in Table 1B. After filtering to only include species pairs which were also present in our viral phylogeny, our data included 763 rows of 172 unique combinations of 19 species. Each row, represented a species pair with an associated edge centrality (calculated from the full networks, before filtering and scaling); pairwise weight (mean = 166.81; SD = 285.87) and SRI (mean = 0.005; SD = 0.005); and, three measures from our viral phylogeny; maximum genetic distance between viral sequences (mean = 0.05; SD = 0.02), and mean Geometric (distance in m; 279121.8; 103676.6)- and temporal-distance in days; 236.72; 115.93), all of which were repeated across networks.

Table 1A. Descriptive statistics for within-year social networks showing the number of species involved in the network (network nodes); the number of edges between species pairs, representing co-occurrence within a recording event, and, the number of recording events. A recording event represents a single survey visit in time and space. **1B.** Network similarity over years: **Upper right matrix** showing Jaccard similarity, the number of shared dyads between years irrespective of edge weight; and, **Lower left matrix**, Spearman rank correlation coefficients between dyadic edge weight between shared dyads, between years. In both cases 1 = perfect correlation and 0 = no relationship.

A. Network structure					B. Network similarity between years					
	Species	Edges	Events			2018	2019	2020	2021	2022
2018	115	4132	354		2018	-	0.67	0.65	0.56	0.56
2019	131	5321	729		2019	0.89	-	0.71	0.64	0.67
2020	127	4938	717		2020	0.86	0.91	-	0.66	0.63
2021	134	6378	782		2021	0.83	0.87	0.86	-	0.73
2022	137	6154	748		2022	0.79	0.85	0.85	0.91	-

Model outputs: We ran two models to test the relationship between wild bird social network structure and HPAI viral phylogenetic distance; the first used weight as a fixed effect and tested for a link between absolute co-occurrence (the number of shared events between a species dyad); and the second used the Simple Ratio Index of a species dyad to measure the extent that two species were recorded together over their opportunity for co-occurrence. We ran two models because pairwise weight and SRI are inherently correlated (Pearson's r = 0.91).

Pairwise weight: We tested the hypothesis that high co-occurrence should result in a greater chance of transmission between a species pair, and therefore closer genetic distance between viral sequences. We found a significant negative effect of pairwise weight on maximum genetic distance (95CI = -0.149 - -0.049; Estimate (or posterior mean) = -0.10), consistent with species that co-occur in the landscape had more closely related viral sequences than those that co-occurred less frequently. Scaled mean

geometric- (95CI = 0.02 - 0.136; Estimate = 0.07) and mean temporal distance (95CI = 0.35 - 0.43; Estimate = 0.39) both had a positive effect on maximum genetic distance, confirming that sequences sampled closer in time and/or space were more similar to one another.

SRI: SRI is a similar measure to pairwise weight, but, as well as shared recording events, SRI also accounts for the opportunity for co-occurrence. A higher SRI is therefore a measure of clustering probability in the social network. We tested the hypothesis that high SRI (highly correlated dyads) should therefore predict close genetic distance, as a proxy for interspecific HPAI virus transmission. Similarly to pairwise weight, we found a negative association between scaled SRI and viral genetic distance (95CI = -0.19 - -0.09; Estimate = -0.14), suggesting that frequent host co-occurrence is associated with closer (maximum) genetic distance between viral sequences. scaled mean geometric- (95CI = 0.01 - 0.012; Estimate = 0.06) and mean temporal distance (95CI = -0.19 - -0.09; Estimate = -0.14) both were positively associated with the maximum genetic distance, again, confirming the assumption that sequences sampled closer in time and/or space were more similar to one an-other. Year did not explain much variance in the model, supporting our assumption that networks constructed between years represent broadly similar structures.

Permutations: To test if the identified associations were the result of community structure, we also rewired network and repeated our models using an expected distribution. In both cases, our observed estimate fell outside of the permuted (non-Bayesian) confidence intervals of the permuted estimates: pairwise weight (95CI = -0.03 - 0.03) and SRI (95CI = -0.015 - 0.019), suggesting that our observed results are unlikely to be the outcome of random chance. The significant positive effects of geometric and temporal distance remained significant predictors of viral genome similarity (see Figure 1:B).

Discussion: We combined a multi-species social network of waterbird co-occurrence from a location in England, United Kingdom, with recurrent HPAI outbreaks in wild birds and poultry, with an extensive database of HPAI viral genome samples. We tested the hypothesis that social proximity predicts the spread of disease through communities of wild animals, to support future surveillance of zoontic and epizootic diseases, prior to their emergence in humans or livestock. We found that both measures of social proximity, edge weight -a measure of raw co-occurrence in the landscape- and Simple Ratio Index (SRI) -a measure of 'connectedness' between two species, accounting for opportunity for co-occurrence- both predicted similarity in HPAI genome sequences. To do this, we accessed two large and open data repositories underscoring the value of such data to research into communities of wild animals. Although we used WeBS data from the British Trust for Ornithology, recent studies have also used similar open-data to infer multi-species networks of wild animals (Albery et al. 2020; Van Doren et al. 2025). Or, similarly, Vickers et al. (2024) used the eBird global repository of bird survey data (Sullivan et al. 2009) to link population dynamics in wild birds with HPAI incursion into poultry. In a social network context, previous studies have demonstrated transmission in simple, single species transmission systems (Hamede et al. 2009; Wilson-Aggarwal et al. 2019; Proboste et al. 2024), or, when applied to traits, in multi-species systems (Luis et al. 2015). Our results suggest, for the first time, that transmission of a disease of pandemic potential is also measurable through a multi-species network of wild animals, using social links as a proxy for transmission. This result is also predicted in the context of host- or environment traits, which drive pathogen transmission because they influence the shape of the social network, facilitating transmission by driving potential hosts into closer proximity (Hamede et al. 2009; Prosser et al. 2023; Jeglinski et al. 2024), facilitating social linkage. Our study demonstrates an empirical baseline for further theoretical predictive modelling of multi-species host-pathogen networks, by using the social links as a proxy for transmission to fill gaps in phylodynamic modelling.

Although our study represents a complex, multi-species transmission system, we did not make assumptions on the role of specific host traits in shaping contagion, within the community or at broader scales. Yet, although we have emperically demonstrated the

pathways of transmission between wild animals, it is host traits that drive transmission through there social links, through traits that influence immuno-competence, or behaviors triggered by the presence of disease in the community (S. Hill et al. 2016; N. Hill et al. 2022; Pearce-Higgins et al. 2023; Jeglinski et al. 2024) or indirectly, by shaping the social network through which disease is transferred, irrespective of the presence of disease (for example, Firth, Sheldon, and Brent 2017; Firth et al. 2017; Albery et al. 2022; Dunning et al. 2023; Schroeder et al. 2024). Our study focused on spread at the landscape scale, for which we used multiple sites within a 50km buffer of a farm with recurrent HPAI outbreaks in England. However, it is also likely that host traits drive disease transmission at different scales, for example long-distance migration has been associated with intercontinental HPAI transmission (Tian et al. 2015; McDuie et al. 2024); Whereas, local outbreaks in poultry have been associated with short-distance dispersal in sedentary game birds(Bourke et al. 2024; Gamża et al. 2024).

Our study focused on the social-links within a community of waterbirds, a natural reservoir of HPAIs with inferred intermediate transmission (Humphreys et al. 2020; Vickers et al. 2024), and for which we had community and viral genome data. We accessed data on community structure from the BTO WeBS which only samples waterbirds using repeated visits and a standardized methodology. As such, the edges in our networks represented co-occurrence between a species pair within a recording event, which we have demonstrated in a social network context (Dunning, Firth, and Ward 2024), predicted similarity in HPAI genomes. However we note that a community of wild animals may include multiple mechanisms of transmission, and our study is appropriate only when applied to passive transmission systems. For example, our HPAI viral genome database also included samples taken from predatory birds, raptors, that had close genetic distances to colonial seabirds (Gamża et al. 2024). However, those links are trophic, rather than social, and likely represent ingestion of infected prey, rather than passive transmission. We therefore suggest that future studies should define network edges by the mechanism of transmission, for example social links, mobility, or predator-prey interactions, to study patterns of transmission.

We were able to use 763 pairwise genome samples, across years, of 172 unique dyads of 19 host species for this study, but we were limited by the availability of genome data for potential host species - our global social network, by comparison, comprised of 8,035 edges between 159 species nodes. Although the sub-graph (blue, within the graph given in Figure 1) is sufficient as a proof of concept here, we suggest passive, rather than reactive, sampling of wild animals where transmission is possible (also suggested by Atkinson et al. 2025) would be beneficial to future study. Combined, our results suggest that waterfowl social network structure, at the landscape scale, is stable over time, and supports our hypothesis that species co-occurrence in the landscape is linked with closer viral genetic similarity, implying measurable transmission through a social network of wild birds.

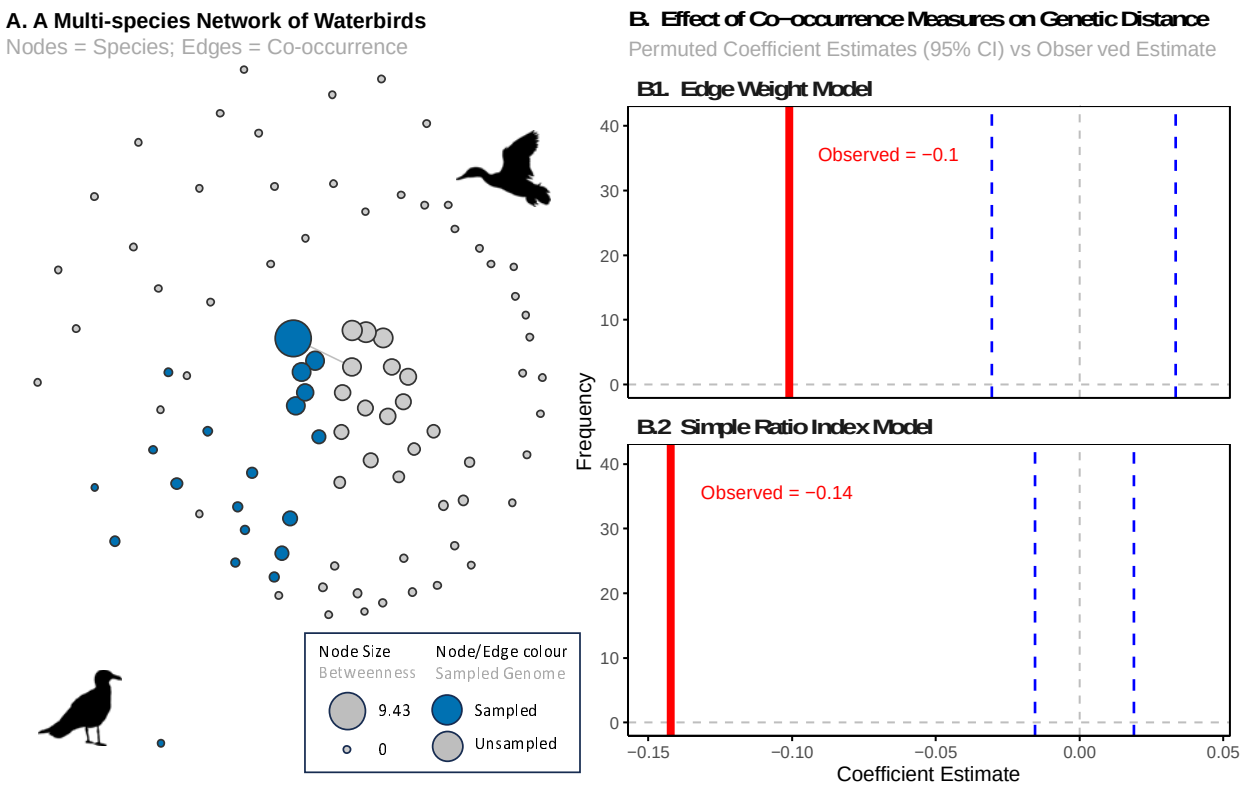

Figure 1. **Panel A.** Of the 159 species in the co-occurrence network, 19 were also associated with a genome for highly pathogenic avian influenza clade 2.3.4.4b, of which we had access to 759 samples. The colour of the nodes and edges denotes that a species pair had viral genome data available, blue, or not, grey. The node size denotes normalised betweenness value, where 9.43, sits on the greatest number of shortest paths between all of dyads in the network, in this case Mute Swan *Cygnus olor*, and 0, on no of the shortest paths (here including Northern Lapwing *Vanellus Vanellus*, Little egret *Egretta garzetta*, and Northern pintail *Anas acuta*). **Panel B.** The expected distribution of permuted estimates in blue, with 95% confidence intervals - blue dotted lines, plotted against the observed estimate - red vertical line, for two measures of network structure – edge weight and Simple Ratio Index. In both cases, the observed estimate falls outside the permuted distribution, suggesting that closer social proximity predicts greater similarity in HPAI viral genome samples. This indicates that our results differ from what is expected when social structure is removed from the network.

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Bibliography:

Albery, Gregory F, Tim H Clutton-Brock, Alison Morris, Sean Morris, Josephine M Pemberton, Daniel H Nussey, and Josh A Firth. 2022. "Ageing Red Deer Alter Their Spatial Behaviour and Become Less Social." Nature Ecology & Evolution 6 (8): 1231–38.

Albery, Gregory F, Evan A Eskew, Noam Ross, and Kevin J Olival. 2020. "Predicting the Global Mammalian Viral Sharing Network Using Phylogeography." Nature Communications 11 (1): 2260.

Albery, Gregory F, Lucinda Kirkpatrick, Josh A Firth, and Shweta Bansal. 2021. "Unifying Spatial and Social Network Analysis in Disease Ecology." Journal of Animal Ecology 90 (1): 45–61.

Andrew, Cassandra L., Shannon L. Russell, Michelle Coombe, James E. A. Zlosnik, Kevin S. Kuchinski, Jessica M. Caleta, Chris Fjell, et al. 2024. "Descriptive Epidemiology and Phylodynamics of the 'First Wave' of an Outbreak of Highly Pathogenic Avian Influenza (H5N1 Clade 2.3.4.4b) in British Columbia and the Yukon, Canada, April to September 2022." Transboundary and Emerging Diseases. https://api.semanticscholar.org/CorpusID:268067430.

Atkinson, Philip W, and Stephen R Baillie. 2024. "Jumping Species and Seasons–the Spread and Impact of Highly Pathogenic Avian Influenza on Seabirds and Waterbirds." Bird Study 71 (4): 289–92.

Atkinson, Philip W., Dawn E. Balmer, Ashley C. Banyard, Jean Duggan, Marco Falchieri, Teresa M. Frost, Elizabeth M. Humphreys, et al. 2025. "Evaluating the Use of

Carcass and Testing Data to Assess the High Pathogenicity Avian Influenza (HPAI) Related Mortality in Wild Birds in the United Kingdom and Crown Dependencies Between 2021–2023." Bird Study 0 (0): 1–19. https://doi.org/10.1080/00063657.2025.2492902.

Bansal, Shweta, Bryan T Grenfell, and Lauren Ancel Meyers. 2007. "When Individual Behaviour Matters: Homogeneous and Network Models in Epidemiology." Journal of the Royal Society Interface 4 (16): 879–91.

Banyard, Ashley C., Fabian Z. X. Lean, Caroline Robinson, Fiona Howie, Glen Tyler, Craig Nisbet, James Seekings, et al. 2022. "Detection of Highly Pathogenic Avian Influenza Virus H5N1 Clade 2.3.4.4b in Great Skuas: A Species of Conservation Concern in Great Britain." Viruses 14. https://api.semanticscholar.org/CorpusID:246338297.

Beck, Kristina B, Ben C Sheldon, and Josh A Firth. 2023. "Social Learning Mechanisms Shape Transmission Pathways Through Replicate Local Social Networks of Wild Birds." eLife 12 (May): e85703. https://doi.org/10.7554/eLife.85703.

Bennison, Ashley, Stacey Adlard, Ashley C Banyard, Freya Blockley, Marcia Blyth, Emma Browne, George Day, et al. 2024. "A Case Study of Highly Pathogenic Avian Influenza (HPAI) H5N1 at Bird Island, South Georgia: The First Documented Outbreak in the Subantarctic Region." Bird Study, 1–12.

Bernstein, Aaron S, Amy W Ando, Ted Loch-Temzelides, Mariana M Vale, Binbin V Li, Hongying Li, Jonah Busch, et al. 2022. "The Costs and Benefits of Primary Prevention of Zoonotic Pandemics." Science Advances 8 (5): eabl4183.

Blagodatski, Artem, Kseniya A Trutneva, Olga Glazova, Olga Mityaeva, Liudmila Shevkova, Evgenii Kegeles, Nikita Onyanov, et al. 2021. "Avian Influenza in Wild Birds and Poultry: Dissemination Pathways, Monitoring Methods, and Virus Ecology." Pathogens 10. https://api.semanticscholar.org/CorpusID:235240633.

Bonneaud, Camille, and Ben Longdon. 2020. "Emerging Pathogen Evolution: Using Evolutionary Theory to Understand the Fate of Novel Infectious Pathogens." EMBO Reports 21 (9): e51374.

Boulinier, Thierry. 2023. "Avian Influenza Spread and Seabird Movements Between Colonies." Trends in Ecology & Evolution. https://api.semanticscholar.org/CorpusID:257172111.

Bourke, Brian P., Robert J. Dusek, Koray Ergunay, Yvonne-Marie Linton, and Sergei V. Drovetski. 2024. "Viral Pathogen Detection in u.s. Game-Farm Mallard (Anas Platyrhynchos) Flags Spillover Risk to Wild Birds." Frontiers in Veterinary Science. https://api.semanticscholar.org/CorpusID:270073602.

Buhnerkempe, Michael G, Mick G Roberts, Andrew P Dobson, Hans Heesterbeek, Peter J Hudson, and James O Lloyd-Smith. 2015. "Eight Challenges in Modelling Disease Ecology in Multi-Host, Multi-Agent Systems." Epidemics 10: 26–30.

Bürkner, Paul-Christian. 2017. "Brms: An r Package for Bayesian Multilevel Models Using Stan." Journal of Statistical Software 80: 1–28.

Burrough, Eric R, Drew R Magstadt, Barbara Petersen, Simon J Timmermans, Phillip C Gauger, Jianqiang Zhang, Chris Siepker, et al. 2024. "Highly Pathogenic Avian Influenza a (H5N1) Clade 2.3. 4.4 b Virus Infection in Domestic Dairy Cattle and Cats, United States, 2024." Emerging Infectious Diseases 30 (7): 1335.

Byrne, Alexander MP, Joe James, Benjamin C Mollett, Stephanie M Meyer, Thomas Lewis, Magdalena Czepiel, Amanda H Seekings, et al. 2023. "Investigating the Genetic Diversity of H5 Avian Influenza Viruses in the United Kingdom from 2020–2022." Microbiology Spectrum 11 (4): e04776–22.

Carlson, Colin J, Gregory F Albery, Cory Merow, Christopher H Trisos, Casey M Zipfel, Evan A Eskew, Kevin J Olival, Noam Ross, and Shweta Bansal. 2022. "Climate Change Increases Cross-Species Viral Transmission Risk." Nature 607 (7919): 555–62.

Clemmons, Elizabeth A, Kendra J Alfson, and John W Dutton III. 2021. "Transboundary Animal Diseases, an Overview of 17 Diseases with Potential for Global Spread and Serious Consequences." Animals 11 (7): 2039.

Coffey, Peter, and Rebecca S Verspoor. 2025. "Case Study of the Impact of an Outbreak of High Pathogenicity Avian Influenza (HPAI) on a Seabird Colony in Flintshire, Wales, United Kingdom." Bird Study, 1–9.

Collier, Melissa, Gregory F Albery, Grant C McDonald, and Shweta Bansal. 2022. "Pathogen Transmission Modes Determine Contact Network Structure, Altering Other Pathogen Characteristics." Proceedings of the Royal Society B 289 (1989): 20221389.

Côté, Isabelle M, and Robert Poulinb. 1995. "Parasitism and Group Size in Social Animals: A Meta-Analysis." Behavioral Ecology 6 (2): 159–65.

Csardi, Gabor, and Tamas Nepusz. 2006. "The Igraph Software Package for Complex Network Research." InterJournal, Complex Systems 1695 (5): 1–9.

Desvars-Larrive, Amélie, Anna Elisabeth Vogl, Gavrila Amadea Puspitarani, Liuhuaying Yang, Anja Joachim, and Annemarie Käsbohrer. 2024. "A One Health Framework for Exploring Zoonotic Interactions Demonstrated Through a Case Study." Nature Communications 15 (1): 5650.

Dunning, Jamie, Terry Burke, Alex Hoi Hang Chan, Heung Ying Janet Chik, Tim Evans, and Julia Schroeder. 2023. "Opposite-Sex Associations Are Linked with Annual Fitness, but Sociality Is Stable over Lifetime." Behavioral Ecology arac124. https://doi.org/https://doi.org/10.1093/beheco/arac124.

Dunning, Jamie, Josh A Firth, and Alastair I. Ward. 2024. "The Spread of HAPI Is a Social Network Problem." PLOS Pathogens.

Falchieri, Marco, Scott M. Reid, Craig S. Ross, Joe James, Alexander M. P. Byrne, Mădălina Zamfir, Ian H. Brown, et al. 2022. "Shift in HPAI Infection Dynamics Causes

Significant Losses in Seabird Populations Across Great Britain." The Veterinary Record 191 7: 294–96. https://api.semanticscholar.org/CorpusID:252753609.

Farine, Damien R. 2017. "A Guide to Null Models for Animal Social Network Analysis." Methods in Ecology and Evolution 8 (10): 1309–20.

Farine, Damien R, and Hal Whitehead. 2015. "Constructing, Conducting and Interpreting Animal Social Network Analysis." Journal of Animal Ecology 84 (5): 1144–63.

Firth, Josh A, Joel Hellewell, Petra Klepac, Stephen Kissler, Adam J Kucharski, and Lewis G Spurgin. 2020. "Using a Real-World Network to Model Localized COVID-19 Control Strategies." Nature Medicine 26 (10): 1616–22.

Firth, Josh A, Joel Hellewell, Petra Klepac, Stephen Kissler, CMMID COVID-19 working group, Adam J Kucharski, and Lewis G Spurgin. 2020. "Combining Fine-Scale Social Contact Data with Epidemic Modelling Reveals Interactions Between Contact Tracing, Quarantine, Testing and Physical Distancing for Controlling COVID-19." MedRxiv, 2020–05.

Firth, Josh A, Ben C Sheldon, and Lauren JN Brent. 2017. "Indirectly Connected: Simple Social Differences Can Explain the Causes and Apparent Consequences of Complex Social Network Positions." Proceedings of the Royal Society B: Biological Sciences 284 (1867): 20171939.

Firth, Josh A, Ben C Sheldon, and Damien R Farine. 2016. "Pathways of Information Transmission Among Wild Songbirds Follow Experimentally Imposed Changes in Social Foraging Structure." Biology Letters 12 (6): 20160144.

Firth, Josh A, Bernhard Voelkl, Ross A Crates, Lucy M Aplin, Dora Biro, Darren P Croft, and Ben C Sheldon. 2017. "Wild Birds Respond to Flockmate Loss by Increasing Their Social Network Associations to Others." Proceedings of the Royal Society B: Biological Sciences 284 (1854): 20170299.

Gamża, Anna, Sam Lycett, Aeron Sanchez, and Rowland Kao. 2024. "Using Sequence Data to Study Spatial Scales of Interactions Driving Spread of Highly Pathogenic Avian Influenza in Great Britain." arXiv Preprint arXiv:2411.10424.

Gao, George F. 2014. "Influenza and the Live Poultry Trade." Science. American Association for the Advancement of Science.

Garamszegi, Laszlo Zsolt, and Anders Pape Møller. 2007. "Prevalence of Avian Influenza and Host Ecology." Proceedings of the Royal Society B: Biological Sciences 274 (1621): 2003–12.

Gómez, José María, Charles L Nunn, and Miguel Verdú. 2013. "Centrality in Primate–Parasite Networks Reveals the Potential for the Transmission of Emerging Infectious Diseases to Humans." Proceedings of the National Academy of Sciences 110 (19): 7738–41.

Hamede, Rodrigo K, Jim Bashford, Hamish McCallum, and Menna Jones. 2009. "Contact Networks in a Wild Tasmanian Devil (Sarcophilus Harrisii) Population: Using Social Network Analysis to Reveal Seasonal Variability in Social Behaviour and Its Implications for Transmission of Devil Facial Tumour Disease." Ecology Letters 12 (11): 1147–57.

Hill, Nichola J., Mary Anne Bishop, Nídia Sequeira Trovão, Katherine M Ineson, Anne Louise Schaefer, Wendy B Puryear, Katherine Zhou, et al. 2022. "Ecological Divergence of Wild Birds Drives Avian Influenza Spillover and Global Spread." PLoS Pathogens 18. https://api.semanticscholar.org/CorpusID:248916359.

Hill, Sarah C, Ruth J Manvell, Bodo Schulenburg, Wendy Shell, Paul S Wikramaratna, Christopher Perrins, Ben C Sheldon, Ian H Brown, and Oliver G Pybus. 2016. "Antibody Responses to Avian Influenza Viruses in Wild Birds Broaden with Age." Proceedings of the Royal Society B: Biological Sciences 283 (1845): 20162159.

Hillemann, Friederike, Ella F Cole, Ben C Sheldon, and Damien R Farine. 2020. "Information Use in Foraging Flocks of Songbirds: No Evidence for Social Transmission of Patch Quality." Animal Behaviour 165: 35–41.

Holmes, Edward C. 2022. "COVID-19—Lessons for Zoonotic Disease." Science 375 (6585): 1114–15.

Humphreys, John M, Andrew M Ramey, David C Douglas, Jennifer M Mullinax, Catherine Soos, Paul Link, Patrick Walther, and Diann J Prosser. 2020. "Waterfowl Occurrence and Residence Time as Indicators of H5 and H7 Avian Influenza in North American Poultry." Scientific Reports 10 (1): 2592.

Jeglinski, Jana W. E., Jude V Lane, S C Votier, Robert W. Furness, Keith C. Hamer, Dominic J McCafferty, Ruedi G. Nager, Megan Sheddan, Sarah Wanless, and Jason Matthiopoulos. 2024. "HPAIV Outbreak Triggers Short-Term Colony Connectivity in a Seabird Metapopulation." Scientific Reports 14. https://api.semanticscholar.org/CorpusID:267545149.

Jones, Kate E, Nikkita G Patel, Marc A Levy, Adam Storeygard, Deborah Balk, John L Gittleman, and Peter Daszak. 2008. "Global Trends in Emerging Infectious Diseases." Nature 451 (7181): 990–93.

Kandeil, Ahmed M., Christopher Patton, Jeremy C. Jones, Trushar Jeevan, Walter N Harrington, Sanja Trifkovic, J. Patrick Seiler, et al. 2023. "Rapid Evolution of a(H5N1) Influenza Viruses After Intercontinental Spread to North America." Nature Communications 14. https://api.semanticscholar.org/CorpusID:258968709.

Karesh, William B, Andy Dobson, James O Lloyd-Smith, Juan Lubroth, Matthew A Dixon, Malcolm Bennett, Stephen Aldrich, et al. 2012. "Ecology of Zoonoses: Natural and Unnatural Histories." The Lancet 380 (9857): 1936–45.

Katoh, Kazutaka, and Daron M Standley. 2013. "MAFFT: Iterative Refinement and Additional Methods." In Multiple Sequence Alignment Methods, 131–46. Springer.

Keck, François, and Andrew Mahon. 2020. "Handling Biological Sequences in r with the Bioseq Package." Methods in Ecology & Evolution 11 (12).

Keesing, Felicia, Lisa K Belden, Peter Daszak, Andrew Dobson, C Drew Harvell, Robert D Holt, Peter Hudson, et al. 2010. "Impacts of Biodiversity on the Emergence and Transmission of Infectious Diseases." Nature 468 (7324): 647–52.

King, Kayla C, Matthew D Hall, and Justyna Wolinska. 2023. "Infectious Disease Ecology and Evolution in a Changing World." Philosophical Transactions of the Royal Society B. The Royal Society.

Klaassen, Marcel, and Michelle Wille. 2023. "The Plight and Role of Wild Birds in the Current Bird Flu Panzootic." Nature Ecology & Evolution 7: 1541–42. https://api.semanticscholar.org/CorpusID:260953954.

Klovdahl, Alden S. 1985. "Social Networks and the Spread of Infectious Diseases: The AIDS Example." Social Science & Medicine 21 (11): 1203–16.

Kostandova, Natalya, Ronan Corgel, Shweta Bansal, Sophie Bérubé, Eimear Cleary, Chelsea Hansen, Matt DT Hitchings, et al. 2025. "Improving Mobility Data for Infectious Disease Research." Nature Human Behaviour, 1–4.

Kostandova, Natalya, Catherine Schluth, Rohan Arambepola, Fatumah Atuhaire, Sophie Bérubé, Taylor Chin, Eimear Cleary, et al. 2024. "A Systematic Review of Using Population-Level Human Mobility Data to Understand SARS-CoV-2 Transmission." Nature Communications 15 (1): 1–12.

Kraemer, Moritz UG, Chia-Hung Yang, Bernardo Gutierrez, Chieh-Hsi Wu, Brennan Klein, David M Pigott, Open COVID-19 Data Working Group†, et al. 2020. "The Effect of Human Mobility and Control Measures on the COVID-19 Epidemic in China." Science 368 (6490): 493–97.

Kruse, Hilde, Anne-Mette Kirkemo, and Kjell Handeland. 2004. "Wildlife as Source of Zoonotic Infections." Emerging Infectious Diseases 10 (12): 2067.

Kuiken, Thijs, Frederick A Leighton, Ron AM Fouchier, James W LeDuc, Joseph S Malik Peiris, Alejandro Schudel, Klaus Stöhr, and ADME Osterhaus. 2005. "Pathogen Surveillance in Animals." Science 309 (5741): 1680–81.

Kulahci, Ipek G, and John L Quinn. 2019. "Dynamic Relationships Between Information Transmission and Social Connections." Trends in Ecology & Evolution 34 (6): 545–54.

Letsholo, Samantha L., Joe James, Stephanie M. Meyer, Alexander M. P. Byrne, Scott M. Reid, Tirumala Bharani Kumar Settypalli, Sneha Datta, et al. 2022. "Emergence of High Pathogenicity Avian Influenza Virus H5N1 Clade 2.3.4.4b in Wild Birds and Poultry in Botswana." Viruses 14. https://api.semanticscholar.org/CorpusID:253859900.

Li, Yao-Tsun, Martin Linster, Ian H. Mendenhall, Yvonne C. F. Su, and Gavin J. D. Smith. 2019. "Avian Influenza Viruses in Humans: Lessons from Past Outbreaks." British Medical Bulletin. https://api.semanticscholar.org/CorpusID:209409528.

Luis, Angela D, Thomas J O'Shea, David TS Hayman, James LN Wood, Andrew A Cunningham, Amy T Gilbert, James N Mills, and Colleen T Webb. 2015. "Network Analysis of Host–Virus Communities in Bats and Rodents Reveals Determinants of Cross-Species Transmission." Ecology Letters 18 (11): 1153–62.

Lupiani, Blanca, and Sanjay M Reddy. 2009. "The History of Avian Influenza." Comparative Immunology, Microbiology and Infectious Diseases 32 (4): 311–23.

Lycett, Samantha J, Florian Duchatel, and Paul Digard. 2019. "A Brief History of Bird Flu." Philosophical Transactions of the Royal Society B 374 (1775): 20180257.

Macgregor, Callum J, Simon Gillings, Dawn E Balmer, Philipp H Boersch-Supan, Sarah J Harris, Hannah FR Hereward, Elizabeth M Humphreys, et al. 2024. "Impacts of Highly Pathogenic Avian Influenza on Seabird Populations in the North Sea Are Detectable in Sea-Watchers' Migration Counts." Bird Study, 1–15.

Malik, Yashpal Singh, Arockiasamy Arun Prince Milton, Sandeep Ghatak, and Souvik Ghosh. 2021. Role of Birds in Transmitting Zoonotic Pathogens. Springer.

Marí Saéz, Almudena, Sabrina Weiss, Kathrin Nowak, Vincent Lapeyre, Fee Zimmermann, Ariane Düx, Hjalmar S Kühl, et al. 2015. "Investigating the Zoonotic Origin of the West African Ebola Epidemic." EMBO Molecular Medicine 7 (1): 17–23.

McDuie, Fiona, Cory T. Overton, Austen A. Lorenz, Elliott L. Matchett, Andrea L. Mott, Desmond A. Mackell, Joshua T. Ackerman, et al. 2024. "Mitigating Risk: Predicting H5N1 Avian Influenza Spread with an Empirical Model of Bird Movement." Transboundary and Emerging Diseases 2024 (1): 5525298.

Motes-Rodrigo, Alba, Gregory F Albery, Josue E Negron-Del Valle, Daniel Philips, Cayo Biobank Research Unit, Michael L Platt, Lauren JN Brent, and Camille Testard. 2025. "A Natural Disaster Exacerbates and Redistributes Disease Risk Among Free-Ranging Macaques by Altering Social Structure." Ecology Letters 28 (1): e70000.

Olival, Kevin J, Parviez R Hosseini, Carlos Zambrana-Torrelio, Noam Ross, Tiffany L Bogich, and Peter Daszak. 2017. "Host and Viral Traits Predict Zoonotic Spillover from Mammals." Nature 546 (7660): 646–50.

Orginization, World Health. 2024. "Pathogens Prioritization: A Scientific Framework for Epidemic and Pandemic Preparedness." https://www.who.int/publications/m/item/pathogens-prioritization-a-scientific-framework-for-epidemic-and-pandemic-research-preparedness.

Pearce-Higgins, James W, Elizabeth M Humphreys, Niall HK Burton, Philip W Atkinson, Chris Pollock, Gary D Clewley, Daniel T Johnston, et al. 2023. "Highly Pathogenic Avian Influenza in Wild Birds in the United Kingdom in 2022: Impacts, Planning for Future Outbreaks, and Conservation and Research Priorities. Report on Virtual Workshops Held in November 2022." BTO Research Report 752.

Plaza, Pablo I, Víctor Gamarra-Toledo, Juan Rodríguez Euguí, and Sergio A Lambertucci. 2024. "Recent Changes in Patterns of Mammal Infection with Highly Pathogenic Avian Influenza a (H5N1) Virus Worldwide." Emerging Infectious Diseases 30 (3): 444.

Pohlmann, Anne, Jacqueline King, Alice Fusaro, Bianca Zecchin, Ashley C. Banyard, Ian H. Brown, Alexander M. P. Byrne, et al. 2022. "Has Epizootic Become Enzootic? Evidence for a Fundamental Change in the Infection Dynamics of Highly Pathogenic Avian Influenza in Europe, 2021." mBio 13. https://api.semanticscholar.org/CorpusID:249887260.

Pohlmann, Anne, Ole Stejskal, Jacqueline King, Sandra Bouwhuis, Florian Packmor, Elmar Ballstaedt, Bernd Hälterlein, et al. 2023. "Mass Mortality Among Colony-Breeding Seabirds in the German Wadden Sea in 2022 Due to Distinct Genotypes of HPAIV H5N1 Clade 2.3. 4.4 b." Journal of General Virology 104 (4): 001834.

Proboste, Tatiana, Abigail Turnlund, Andrew Bengsen, Matthew Gentle, Cameron Wilson, Lana Harriott, Richard A Fuller, Darren Marshall, and Ricardo J Soares Magalhães. 2024. "Quantifying Feral Pig Interactions to Inform Disease Transmission Networks." bioRxiv, 2024–08.

Prosser, Diann J, Claire S Teitelbaum, Shenglai Yin, Nichola J Hill, and Xiangming Xiao. 2023. "Climate Change Impacts on Bird Migration and Highly Pathogenic Avian Influenza." Nature Microbiology 8 (12): 2223–25.

Reid, Scott M, Alexander MP Byrne, Fabian ZX Lean, Craig S Ross, Andrei Pascu, Richard Hepple, Maria Dominguez, et al. 2024. "A Multi-Species, Multi-Pathogen Avian Viral Disease Outbreak Event: Investigating Potential for Virus Transmission at the Wild Bird–Poultry Interface." Emerging Microbes & Infections 13 (1): 2348521.

Ryding, Sara, Tobias A Ross, and Marcel Klaassen. 2025. "Predicting High Pathogenicity Avian Influenza H5N1 Susceptibility in Wild Birds, with Special Reference to Australia."

Sah, Pratha, Stephan T Leu, Paul C Cross, Peter J Hudson, and Shweta Bansal. 2017. "Unraveling the Disease Consequences and Mechanisms of Modular Structure in Animal Social Networks." Proceedings of the National Academy of Sciences 114 (16): 4165–70.

Sah, Pratha, Janet Mann, and Shweta Bansal. 2018. "Disease Implications of Animal Social Network Structure: A Synthesis Across Social Systems." Journal of Animal Ecology 87 (3): 546–58.

Sah, Ranjit, Shriyansh Srivastava, Sachin Kumar, Rachana Mehta, Suzanne Donovan, Leandro Sierra-Carrero, Camila Luna, et al. 2024. "Concerns on H5N1 Avian Influenza Given the Outbreak in US Dairy Cattle." The Lancet Regional Health–Americas 35.

Schroeder, Julia, Jamie Dunning, Alex Hoi Han Chan, Heung Ying Janet Chik, and Terry Burke. 2024. "Not so Social in Old Age: Demography as One Driver of Decreasing Sociality." Philosophical Transactions B 379 (1916): 20220458.

Sidik, Saima May. 2023. "Bird Flu Outbreak in Mink Sparks Concern about Spread in People." Nature 614: 17. https://api.semanticscholar.org/CorpusID:256272784.

Stokstad, E. L. Robert. 2022. "Deadly Bird Flu Establishes a Foothold in North America." Science 377: 912–12. https://api.semanticscholar.org/CorpusID:251844031.

Sullivan, Brian L, Christopher L Wood, Marshall J Iliff, Rick E Bonney, Daniel Fink, and Steve Kelling. 2009. "eBird: A Citizen-Based Bird Observation Network in the Biological Sciences." Biological Conservation 142 (10): 2282–92.

Sun, Xiangdong, Nina Yu-Hsin Kung, Lu Gao, Yongjun Liu, Songhe Zhan, Xin Qi, Xin Wang, Xianmin Dong, Zhining Jia, and Roger Stewart Morris. 2018. "Social Network Analysis for Poultry HPAI Transmission." Transboundary and Emerging Diseases 65 (6): 1909–19.

Team, R Core. 2023. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Teitelbaum, Claire S, Nicholas M Masto, Jeffery D Sullivan, Allison C Keever, Rebecca L Poulson, Deborah L Carter, Abigail G Blake-Bradshaw, et al. 2023. "North American Wintering Mallards Infected with Highly Pathogenic Avian Influenza Show Few Signs of Altered Local or Migratory Movements." Scientific Reports 13 (1): 14473.

Tian, Huaiyu, Sen Zhou, Lu Dong, Thomas P Van Boeckel, Yujun Cui, Scott H Newman, John Y Takekawa, et al. 2015. "Avian Influenza H5N1 Viral and Bird Migration Networks in Asia." Proceedings of the National Academy of Sciences 112 (1): 172–77.

Tremlett, Constance J, Ian R Cleasby, Mark Bolton, and Linda J Wilson. 2025. "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.

Uhart, Marcela M, Ralph E. T. Vanstreels, Martha I. Nelson, Valeria Olivera, Julieta Campagna, Victoria Zavattieri, Philippe Lemey, Claudio Campagna, Valeria Falabella, and Agustina Rimondi.