

Long-Term Wetland Habitat Loss and H5N1 Outbreaks in Domestic Poultry in the United States,
2020 - 2026

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Abstract

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The emergence of the H5N1 2.3.4.4b clade virus in October 2020 has driven the world into a devastating H5N1 panzootic that has led to the deaths of millions of birds across the world¹. In December 2021, this panzootic strain was detected in the United States, since which it has affected over 58 million birds¹. In this study, we sought to characterize how wetland loss over time affected the odds of H5N1 outbreak occurrence. Using spatiotemporal modeling, we found that annual wetland loss over time within 10 km of a given location is associated with increased risk of H5N1 outbreak occurrence. Our results indicate that annual losses in wetland habitat increase the risk of H5N1 outbreaks in the surrounding regions. This study provides potential evidence that wetland loss reduces the productivity of wetland habitats that migratory birds rely on for resources, pushing them to travel outside traditional wetland breeding and wintering sites to meet their nutritional needs and spreading H5N1 to domestic poultry through direct and indirect means.

Introduction:

Avian influenza viruses (AIVs) are zoonotic influenza A viruses that primarily infect birds with varying levels of severity²⁻⁴. Although AIVs rarely infect humans, pandemic AIV strains capable of spreading between humans have emerged in the past. One such example was the 1918 H1N1 AIV pandemic that led to the deaths of an estimated 50 million people². An AIV strain that poses a significant threat to humans and birds alike in the present day is H5N1. This highly pathogenic avian influenza (HPAI) virus has the ability to cause severe illness and death in humans and birds alike. Since its discovery in 1996, outbreaks of H5N1 have led to deaths of hundreds of millions of birds and hundreds of humans^{1,2,5}. The emergent H5N1 2.3.4.4b clade is the cause of an ongoing panzootic that has spread to 114 countries and led to the deaths of tens of millions of birds in one of the largest avian influenza outbreaks in recorded history⁵⁻⁷. This outbreak reached the United States in December 2021, since which over 58 million birds have been affected¹.

Unlike previous H5N1 outbreaks, the current clade 2.3.4.4b panzootic strain has demonstrated sustained transmission amongst mammals, reflecting a startling development in the virus's evolution⁵. While human-to-human transmission of H5N1 is exceedingly rare, the virus's high fatality rate in humans (approximately 50%) coupled with its increasing ability to spread between mammals raises concerns about its pandemic potential^{5,8}. For this reason, it is imperative to prevent H5N1 spillover events from birds to humans, as the reassortment of avian H5N1 strains with human influenza viruses allows H5N1 can mutate to effectively spread between humans⁹. One way to reduce these events is by reducing H5N1 outbreaks in domestic poultry, a significant source of zoonotic transmission of AIVs to humans³. Domestic poultry are thought to be infected with H5N1 by coming into contact with wild waterfowl, such as ducks and geese, which are natural reservoirs for the virus^{4,10}. These interactions, and the overall spread of H5N1 across avian populations, are thought to be linked to waterfowl migration when birds can carry and spread diseases along flyways spanning hundreds of miles¹¹. This has been supported by Lee *et al.*, (2020) which used telemetry tracking of waterfowl to show that poultry farms within the regions used by waterfowl for feeding and resting during migration were at a greater risk for H5N1 outbreak occurrence compared to farms outside of those regions¹².

Migratory waterfowl prefer to feed and rest in wetlands throughout migration¹³. Wetlands are habitats at the transition between terrestrial and aquatic environments, where the water table is at or near the soil surface¹⁴. These environments occur throughout freshwater and saltwater ecosystems in or around bodies of water including ponds, beaches, rivers, and lakes¹⁴. The importance of wetlands to biodiversity and conservation cannot be understated. Approximately 50% of species protected under the U.S. Endangered Species Act are wetland-dependent, including approximately 80% of all protected birds in North America¹⁵. Waterfowl, waders, and shorebirds in particular, utilize wetlands for food, shelter from predators, and breeding grounds during seasonal migration¹⁶. One of the most important ways migratory waterfowl use wetlands during migration is as short-term stopover sites¹³. Time spent at numerous stopover sites may account for up to 85% of a bird's total migration, where they often spend several days regaining energy and preparing for the next leg of their journey by resting and refueling¹³. However, time spent at these locations may also be used for energetically costly activities such as courting mates, molting, and confronting adverse weather, emphasizing the

need for migratory waterfowl to replenish their energy stores at these locations¹³. Wetlands also act as longer-term breeding and wintering sites for migratory waterfowl where they can spend up to months at a time^{15,17,18}. As such, migrating waterfowl require wetlands to provide nutrients to refuel throughout their migratory journeys and to support them for extended stays.

At the time of the settlement of the United States by European colonizers, approximately 215 million acres of wetland habitat covered approximately 11.34% of the nation^{19,20}. By 2019, wetland coverage has been halved, to approximately 116 million acres; furthermore, the rate of wetland loss is accelerating: between 2009 and 2019 wetland loss was 50% greater than wetland loss between 2004 and 2009¹⁴. Anthropogenic activity, particularly agricultural and urban expansion and road construction, is a major driver of wetland loss in the US^{18,21}. Climate change has also been a contributing factor, as storms and rising sea levels along with drought erode and dry out wetlands, respectively¹⁸. Throughout the first half of the 20th century, drainage and filling of wetlands for agricultural purposes was the primary contributor for wetland loss with approximately 500,000 acres being lost per year. Net wetland loss has reduced since then, however, as agricultural development dropped to the second largest source of wetland loss in the second half of the 20th century after rural development¹⁴. Between 2009 to 2019, approximately 67,000 acres of wetland were lost each year, a time period during which agricultural development was the second largest contributor of freshwater wetland loss, behind only upland forested plantations¹⁴.

While the rate of wetland loss has reduced significantly since the 1950s, continued wetland loss still poses a major threat to migratory waterfowl by reducing the number and quality of stopover, wintering, and breeding sites along migratory flyways^{16,17,22}. Newton (2004) describes a density-dependent mechanism through which migratory waterfowl fill habitat sequentially when choosing wintering and breeding sites, with the best habitats reaching capacity first, forcing birds arriving later in the season to settle in progressively less attractive habitats²². Even under ideal conditions, obtaining enough nutrients to support metabolic needs at stopover sites can be difficult due to competition for resources and depletion of available food over time²². The degradation of higher quality sites can reduce their carrying capacity, forcing more and more migratory waterfowl to poorer quality sites for both short and long-term use. Additionally, Guo *et al.*, (2024) propose that wetland loss forces waterfowl out of their preferred stopover sites, concentrating migratory birds where resources still remain, such as wildlife refuges and protected land²³. With time, these sites experience significant resource depletion as their use increases¹³. Increased waterfowl concentration at these sites also has impacts on disease transmission amongst birds. This was seen in Gaidet *et al.*, (2011) which showed that increased waterfowl density was associated with increased AIV prevalence, potentially caused by increased contact rates between birds²⁴.

As a result, migratory waterfowl must look to alternate habitats to meet their resource needs. Farmlands offer food, water, and safety from predation, and those in close proximity to wetlands are frequently visited by migratory waterfowl^{16,25}. McDuie *et al.*, (2022) found that 11 dabbling ducks, including cinnamon teals, mallards, and northern pintails, equipped with GPS trackers regularly traveled between commercial cattle and poultry holdings and adjacent wetlands over the course of five years²⁵. Pearse *et al.*, (2013) documented repeated instances of white-fronted geese and snow geese roosting in Nebraska wetlands while flying to cornfields

to forage²⁶. Poultry farms offer water in the form of puddles, canals, and ditches, and food in the form of spilled feed, drying feed, and insects in manure²⁷. The regular transit of waterfowl between wetlands and farms observed in McDuire *et al.*, (2022) could suggest that migratory waterfowl may frequent farms to make up for a lack of food in wetland roosting locations²⁵. When waterfowl forage for food on farms or cropland, they have the potential to spread H5N1 to domestic poultry and other birds in the vicinity²⁸. Camera trap data show that direct contact between wild waterfowl and domestic poultry in commercial operations is uncommon^{10,27}. However other farm birds, such as magpies or house sparrows, do have regular and close contact with commercial poultry. These birds may serve as bridge hosts, becoming infected with H5N1 via contact with contaminated excreta from visiting waterfowl and subsequently infecting domestic poultry by entering enclosures directly (facilitated by their small size)^{10,27}. Additionally, infected droppings from waterfowl and bridge hosts can contaminate water or feed used by poultry in commercial poultry operations²⁷. Poultry operations such as backyard flocks which have less stringent biosecurity measures are even more susceptible for infection²⁹.

Collectively, this evidence suggests a potential mechanism through which wetland loss could increase the risk of H5N1 outbreaks by increasing the reliance of migratory waterfowl on agricultural land for resources. This could subsequently increase the frequency of contacts between waterfowl and bridge hosts or domestic poultry. However, few studies have used changes in land cover over time to study the temporal relationship between wetland loss, proximity to farmland and likelihood of H5N1 disease outbreaks. Most studies have only partially studied this relationship or theorized its existence. For instance, Wu *et al.*, (2020) found that proximity to highly protected Ramsar wetland sites in China was associated with decreased H5N1 outbreaks in poultry, theorizing that reduced human encroachment both excludes domestic birds from migratory waterfowl habitat and eliminates the “pull” of waterfowl to agricultural settings³⁰. Additionally, in a longitudinal study of comb ducks in the Inner Niger Delta, Cappelle *et al.*, (2011) showed that predicted contacts between domestic and wild poultry increased in the delta when natural wetlands dry out, pulling waterfowl into artificially irrigated fields where villagers let poultry roam freely³¹. This points to an association between wetland loss and increased contact between wild and domestic waterfowl, but stops short of linking H5N1 outbreaks with wetland loss. In a case-control study comparing H5N1 risk factors between farms with and without H5N1 detections in poultry, Green *et al.*, (2023) found that H5N1 outbreak risk was elevated when wild waterfowl or shorebirds were sighted in the vicinity of the farm (OR = 7.6, 95% CI: 1.3, 42.8) and when wild birds were able to access feed (OR = 6.2, 95% CI: 1.2, 31.9)³². This finding suggests that the risk of an H5N1 outbreak on a poultry farm is elevated when waterfowl visit the farm to forage, but does not address wetland loss directly. Together, however, these findings suggest that wetland degradation in the vicinity of farmland may be critical to the ecology of avian influenza, and that they may be key sites advancing the spread of H5N1 in domestic flocks. In this study, we look to expand on this work by investigating how degradation of wetland habitat during the course of the 21st century has affected the dynamics of avian influenza in domestic poultry. We do this by characterizing the association between wetland loss—annual and cumulative—in the US and H5N1 outbreaks in domestic poultry in the vicinity of that loss. By characterizing the relationship between wetland loss and H5N1 outbreak odds, we look to improve the understanding of how long-term anthropogenic change affects AIV spillover into domestic poultry.

Methods:

Outcome:

The outcome of interest was outbreaks of H5N1 in domestic poultry in the United States between 2022 and 2026. An outbreak was defined as one or a cluster of cases within a 20 km radius within the same calendar year. Data for all reported animal H5N1 outbreaks are available from the UN Food and Agricultural Organization (FAO) EMPRES-i Global Animal Disease Information System database⁶. For each outbreak or “case” location, 3 points within 200 and 300 km of the case location were randomly selected as control locations using GPS coordinates logged for each outbreak in the EMPRES-i database.

Exposure:

The exposure of interest was change in wetland area, parameterized as (a) percent annual wetland change for each year from 2000 to 2022, and (b) percent cumulative wetland change between 2000 and 2022. Data on wetland cover was derived from the GLC_FCS30D dataset in Google Earth Engine (GEE)³³. This dataset, derived from Copernicus Landsat imagery, classified land cover across the surface of the Earth into one of 36 categories with a resolution of 30 square meters per pixel between 1985 to 2022. Land cover classification is available annually between 2000 to 2022. Pixels classified as “swamp”, “marsh”, “flooded flat”, “saline”, “mangrove”, “salt marsh”, or “tidal flat” were included as wetland.

Each case and control point was used as a centroid for buffer zones with radii of 10, 25, and 50 km, within which we calculated the annual percent and cumulative change in wetland area. Because the GLC_FCS30D database only extends until 2022, we imputed annual and cumulative changes in wetland area between 2023 and 2026 as the corresponding average from 2000-2022. Additionally, the `inla.group` function was used to discretize response values for annual and cumulative wetland percent change into 100 equidistant probability quantiles throughout the range of the responses for the two variables. The binning approach was used to reduce the computational load needed to fit an INLA model to our ~90,000 observation dataset.

Covariates:

Confounders were defined *a priori* based on previous research detailing the associations between each covariate, the exposure, and the outcome. A summary of these associations is presented below in a directed acyclic graph (DAG):

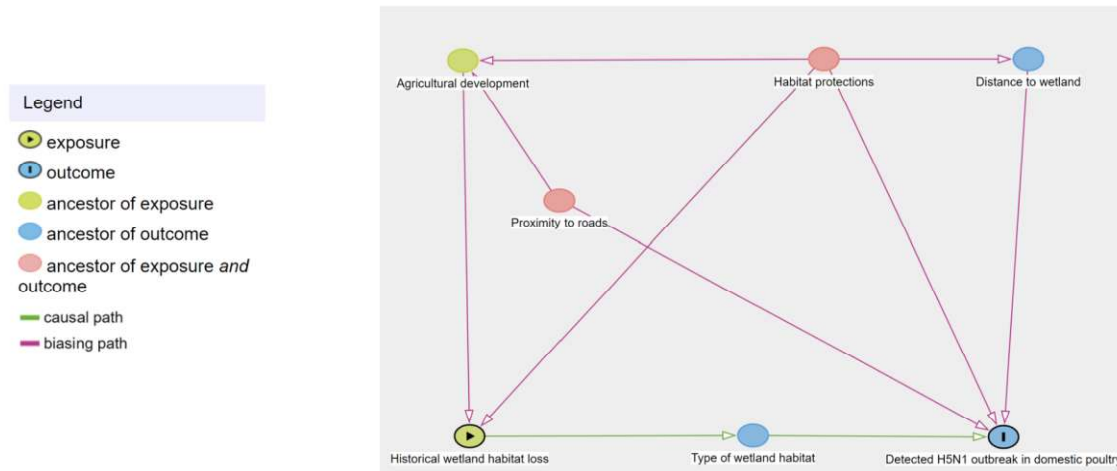


Figure 1: DAG detailing associations between the exposure, outcome, and related covariates.

Ancestors of the exposure and outcome in Figure 1 are variables that have a causal effect on exposure and outcome, respectively. Of these variables, proximity to roads, habitat protections, agricultural development, type of wetland habitat, and distance to the nearest wetlands were categorized as confounders given existing associations between each variable and the exposure as well as the outcome. Proximity to roads was considered a confounder, as the commercial transport of poultry via roads provides an avenue for H5N1-infected birds to spread the virus to healthy flocks³⁴. Additional studies also implicate road construction as a direct and indirect contributor to wetland loss over time²¹. Proximity to roads was calculated as the minimum distance between each case and control point to the nearest road at the start of the outbreak using data from the U.S. Census Bureau TIGER geodatabase³⁵.

Habitat protections are thought to decrease H5N1 transmission to domestic poultry by reducing their contact with wild waterfowl³⁰. Given that land protections also reduce the commercial and industrial activity in protected areas, we assume *a priori* that land protections also provide a protective effect against wetland habitat loss. Habitat protection was measured by calculating the percentage of each buffer zone classified as a protected area at the start of the outbreak by the International Union for Conservation of Nature (IUCN). Protected land was identified using the geospatial United States Protected Areas Database (PAD) version 3.0³⁶.

The demand for farmland has led to the conversion of wetland habitat to dry cropland in the United States and throughout the world for decades, in part to meet the demand for growing populations.^{18,37}. Additionally, previous studies have shown that recently converted croplands act as stopover sites during bird migration³⁸. This provides an opportunity for H5N1 to spread amongst wild waterfowl at the sites and subsequently into domestic birds in the surrounding areas³⁸. Agricultural development was calculated as percent change in cropland between two consecutive years in each buffer zone, for each year from 2000-2022. Pixels classified as "Rainfed cropland", "Herbaceous cropland", "Tree or shrub cover (Orchard) cropland", or "Irrigated cropland" in the GLC_FCS30D database were deemed to be cropland. The same time coverage limitations inherent to the GLC_FCS30D database applied for annual agricultural development as for the annual wetland change and cumulative wetland change variables. To

best estimate agricultural development from 2023 to 2026, the percent change in agricultural area for 2023 to 2026 for each buffer zone was set by averaging the annual percent change in agricultural area for each year between 2000 to 2022, assuming a constant rate of change in agricultural land change after the start of the outbreak in 2022 to the current day in 2026.

Another confounder in this study was distance to the nearest wetland. Previous studies have shown that H5N1 outbreak likelihood was inversely correlated with distance to the nearest wetland³⁴. Additionally, we assume *a priori* that wetland loss caused by human activity is due to human encroachment, and this decreases the distance and increases the proximity between areas where humans live and wetlands. Distance to the nearest wetland was calculated as the minimum distance between each case and control location to the nearest 30 square meter wetland pixel. The rgee package in R was used to break down the GEE image for 2022 into tiles which were stitched into a full raster image which was subsequently converted into a raster mask using the terra and raster packages. This mask, which only encoded data for pixels classified as wetlands, was imported into QGIS and subject to the polygonize function, converting each 30 square meter wetland pixel into a polygon. R was then used to determine the minimum distance to the nearest wetland by calculating the minimum distance between each case and control point to the nearest wetland polygon centroid.

The last confounder was the type of wetland habitat. Wetland loss is not uniform amongst saltwater and freshwater ecosystems, as between 2009 and 2019, the United States Fish and Wildlife Service calculated an overall 0.2% net loss in freshwater wetlands as compared to an overall 0.5% net loss in saltwater wetlands¹⁴. Additionally, studies have shown that the H5N1 virus is significantly less stable in salt water compared to fresh water³⁹. Given that waterborne transmission is a major driver of H5N1 spread, we would expect that H5N1 spreads more effectively in freshwater wetlands⁴⁰. Wetland type was calculated as the percentage of wetlands classified as freshwater wetlands (swamp, marsh, or flooded flat) at the start of the outbreak in 2022.

Model Description:

Outbreaks of H5N1 in domestic poultry between 2022 and 2026 were modeled to follow a binomial distribution:

$$Y_i | p(s_i) \sim \text{Binomial}[p(s_i)]$$

Where:

- Y_i is the outcome of H5N1 outbreak occurrence
- $p(s_{i,t})$ is the probability of an outbreak occurring at location s_i in year t , with i indexing buffer zones $i = 1, \dots, n$, and t indexing year of observation with $t = 1, \dots, T$.

The model for $p(s_{i,t})$ is given by the following generalized additive model (GAM):

$$p(s_{i,t}) = \beta_0 + f(AWL(s_{i,t})) + f(CWL(s_{i,t})) + f(AAD(s_i)) + \beta_4 DR(s_{i,2022}) + \beta_5 DWL(s_{i,2022}) + \beta_6 PL(s_{i,2022}) + \beta_7 FW(s_{i,2022}) + u_i + \varepsilon_t$$

Where:

- β_0 is the intercept

- annual percent change in wetland loss (AWL), agricultural development (AAD), and cumulative percent wetland loss (CWL), are modeled using random walk 2 (RW2) smoothing functions over time
- distance to nearest road (DR) and wetland (DWL), percent protected land in 2022 (PL), and proportion of wetlands classified as freshwater in 2022 (FW) are modeled as fixed effects.
- u_i is the spatial random effect, modeled as a Gaussian-Markov Random Field with variance τ , range κ , and smoothness parameter, ν

$$u_i \sim GMRF(\tau, \kappa, \nu)$$
- ε_t is the temporal random effect, modeled as an autoregressive model of order 1 (AR1) with variance of σ_ε^2

$$\varepsilon_1, \dots, \varepsilon_T \mid \sigma_\varepsilon^2 \sim AR1(\sigma_\varepsilon^2)$$

The RW2 smoothing effect is modeled as:

$$f(x(s_{i,t+1})) - 2f(x(s_{i,t})) + f(x(s_{i,t-1})) \sim N(0, \sigma_x^2)$$

Where:

- $x \in \{AWL, AAD, CWL\}$
- σ_x^2 is the precision of x
- $t = 2, \dots, T$

This model was implemented using integrated nested Laplace approximation via the INLA package in R.

INLA Configuration and SPDE Specifications:

The spatial random effect caused by outbreak location was implemented by using the Stochastic Partial Differential Equation (SPDE) method. A spatial Gaussian Markov Random Field was created using nodes defined by the coordinates of case and controls and a two layer triangular mesh. Specifications on the spatial field placed limitations on the maximum edge length of mesh triangles and the shortest possible distance between nodes.

The prior for the spatial range, random field was set as follows:

$$P(r < 100,000) = 0.90 = \frac{\sqrt{8\nu}}{\kappa}$$

Additionally, a penalized complexity (PC) prior was used for the standard deviation, σ , of the random field.

$$P(\sigma > 3) = 0.01 = \tau$$

These priors set the probability of the spatial range (the distance at which two observations are statistically independent) being greater than 100 km at 10% and the probability of the standard deviation of the spatial latent effect being greater than 3 at 1%. The prior range was based on a previous study of H5N1 outbreaks in ducks which found spatial dependency to drop off after 60 km⁴¹. The resulting mesh was used to create a projector matrix for all case and control locations

which was passed to data stacks for prediction and estimation. The estimation stack contained all covariates and response data between 2000 to 2025, while the prediction data stack contained covariates for 2026. These stacks were combined into an overall data stack used for the INLA function.

Analysis:

To assess whether wetland loss was associated with H5N1 outbreak probability, we extracted the odds ratio, given by the mean value of the RW2 smoothing function over values of annual and cumulative wetland loss drawn from the posterior distribution. This was done at 100 values corresponding to the 1st to 100th percentile of the percent wetland gain for annual and cumulative wetland loss. We subsequently generated exposure-response curves for both exposure variables. The odds ratios and 95% credible intervals (95% CIs) for H5N1 outbreak probability calculated for each response value of annual and cumulative percent wetland loss were used to determine which, if any, levels of observed wetland loss were associated with H5N1 outbreak probability. An association between wetland loss and H5N1 outbreak odds was statistically significant when the 95% CI for the odds ratio excluded the null, $OR = 1$.

Results:

Sample characteristics:

Altogether, 879 outbreaks at 863 distinct locations were identified. A total of 159, 42, and 18 buffer zones were removed from the 10 km, 25 km, and 50 km datasets, respectively, as calculating the percent change in wetland area at these sites required dividing by zero for at least one time interval. The locations of cases and controls are presented in Figure 3, while the spatiotemporal distribution of cases is shown in Figure 2. These figures show that H5N1 outbreaks occurred primarily in the midwest and along the coasts. The temporal distribution of cases shown in Figure 4 indicates that incident outbreaks fell sharply after the first year of the outbreak before spiking again in 2025. Incident outbreaks appear to be far lower in 2026 than 2025, but Figure 4 only reflects outbreaks reported through April 28th, 2026, and is not representative of all outbreaks reported in 2026. Descriptive statistics are presented in Tables 1a to 1c.

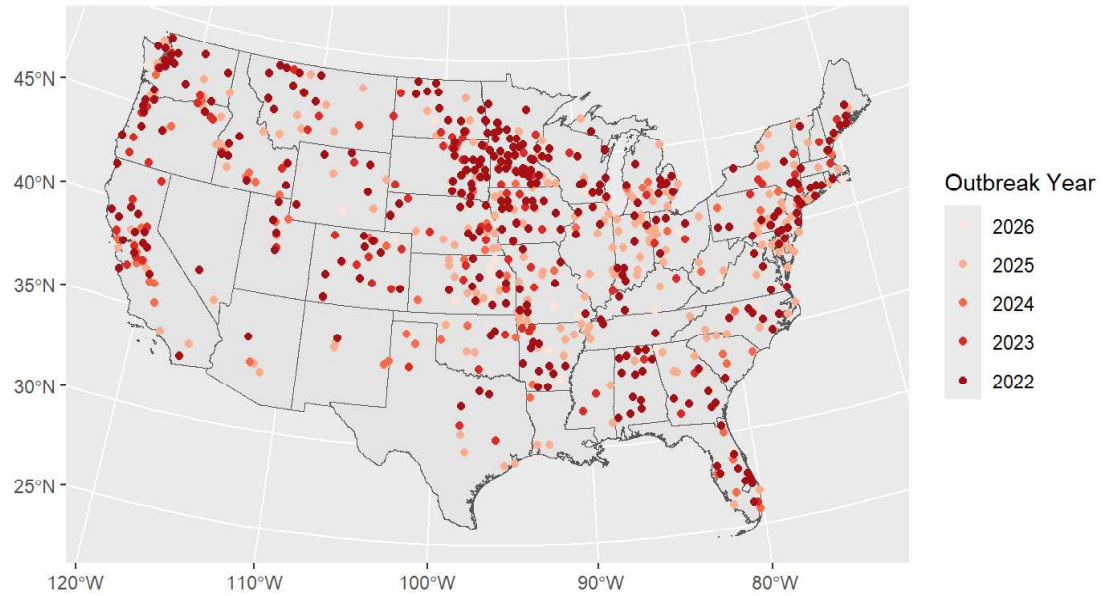


Figure 2: Location of H5N1 outbreaks in domestic poultry in the United States, 2022 - 2026

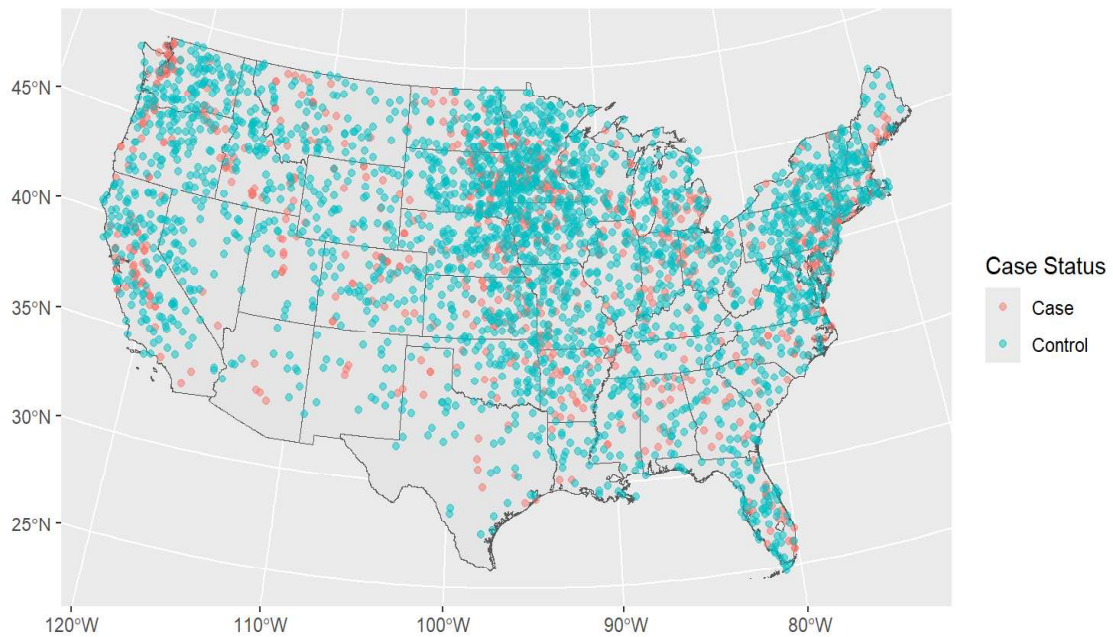


Figure 3: Case and Control Locations

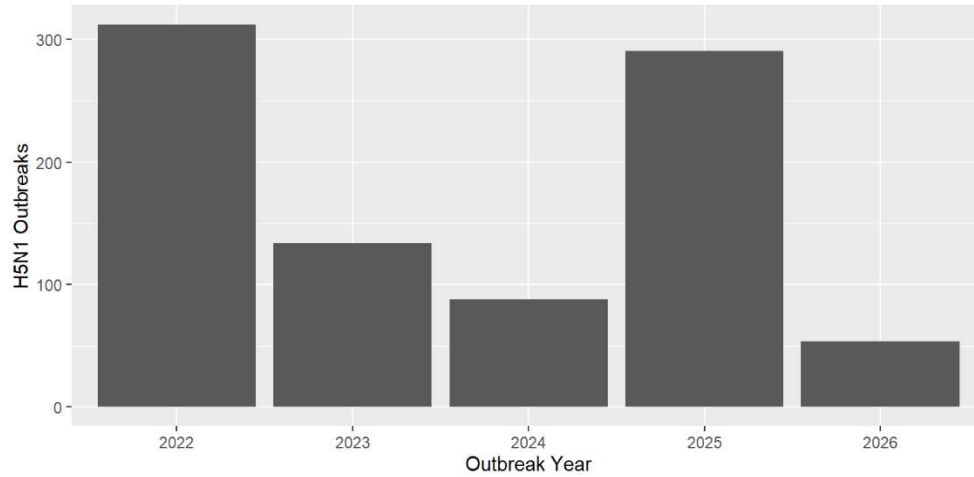


Figure 4: H5N1 outbreaks by year

Table 1: Descriptive statistics. Values for the mean, standard deviation, median, and range were calculated for all years combined.

Variable	10km buffer		25km buffer		50km buffer	
	Mean (sd)	Median (range)	Mean (sd)	Median (range)	Mean (sd)	Median (range)
Distance to the Nearest Wetland (meters)	1973 (6203)	1 (0.59,77750)	2139 (6771)	1 (0.59,106161)	2136 (6768)	1 (0.59,106161)
Protected Land Proportion	0.03 (0.15)	0 (0,1)	0.04 (0.15)	0 (0,1)	0.04 (0.14)	0 (0,1)
Freshwater Wetland Proportion	0.18 (0.38)	0 (0,1)	0.18 (0.38)	0 (0,1)	0.18 (0.38)	0 (0,1)
Distance to the Nearest Road (meters)	6807 (22181)	1 (0.4,272181)	7131 (23053)	1 (0.4,252300)	7118 (23021)	1 (0.4,252300)
Annual Wetland Change Proportion	0.03 (0.27)	0 (-0.93,2.5)	0.01 (0.18)	0 (-0.58,1.4)	0.01 (0.14)	0 (-0.44,0.89)
Wetland Cumulative Change	1.2 (0.86)	1.1 (0,13)	1.1 (0.5)	1.1 (0,6.1)	1.1 (0.37)	1.1 (0.02,4.4)
Annual Cropland Change Proportion	0.01 (0.07)	0 (-0.27,0.62)	0.01 (0.05)	0 (-0.16,0.32)	0.01 (0.03)	0 (-0.1,0.19)

Main Effects:

10km buffer

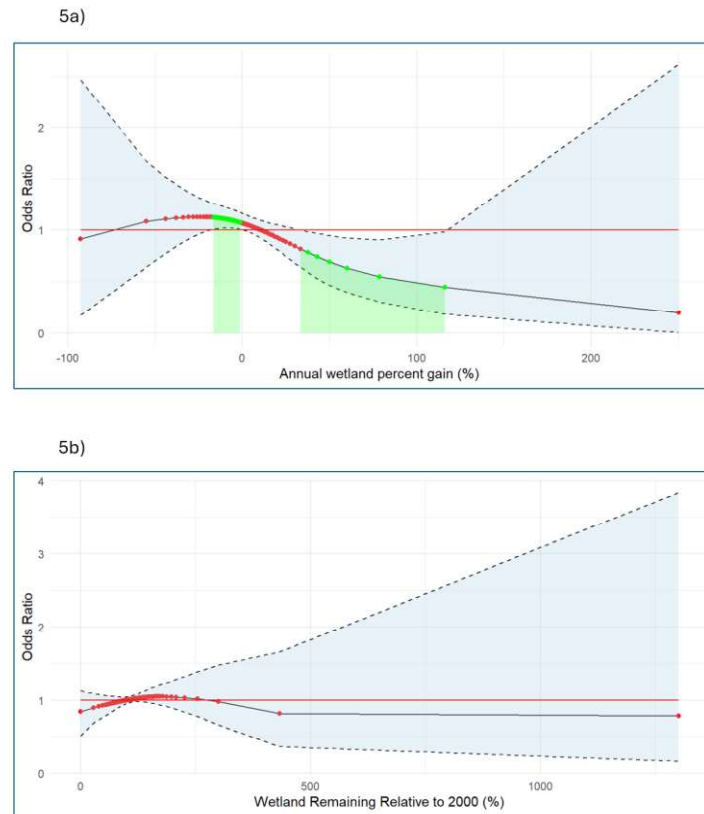


Figure 5: Exposure-response (H5N1 outbreak odds) curve, 10km buffer. Odds ratios calculated as the mean of the posterior distribution over values of wetland gain). Random walk 2 smoothing function is shown as a solid black line, with 95% credible interval bounds shaded in blue and bordered by black dotted lines. **5a:** Mean odds ratio for annual percent wetland gain; **5b:** Mean odds ratio for cumulative wetland gain between 2000 and 2026. **Red dots:** values of the exposure for which the corresponding OR is non-significant. **Green dots:** values of the exposure for which the corresponding OR is significant. **Green shading:** Intervals of the exposure for which the corresponding odds ratio is statistically significant intervals are shaded in green. **Red line:** The null odds ratio $OR = 1$

Results for the 10km buffer are shown in Figure 5. The RW2 smoothing functions in Figures 5a and 5b followed the same pattern where the odds ratio increased and peaked before gradually decreasing with increased wetland gain. Annual wetland change had a positive association with H5N1 outbreak odds between the interval of 55% loss and 9.8% gain. This association was significant in the range of 16.4% loss ($OR = 1.12$, 95% CI: 1.01, 1.26) to 1.14% loss ($OR = 1.07$, 95% CI: 1.01, 1.16), the magnitude of which ranged from 7 to 12% elevated outbreak odds per every one percent increase in wetland loss within the interval [Table 2].

Annual wetland change had a negative association with H5N1 outbreak odds outside of this range. This association was statistically significant within the range of 37.6% ($OR = 0.78$, 95% CI: 0.59, 0.98) and 116%, ($OR = 0.45$, 95% CI: 0.19, 0.98) wetland gain. This indicates that an annual increase in wetland area between 37.6% and 116% is associated with a 22% to

57% decreased odds of H5N1 outbreaks for every one percent increase in wetland gain [Table 2].

Table 2: Annual Wetland Gain Significant Response Intervals, 10 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-16.4%, -1.14%	1.07 (1.00, 1.16)	1.12 (1.01, 1.26)
37.6%, 116%	0.78 (0.59, 0.98)	0.45 (0.19, 0.98)

By contrast, there was no significant effect of cumulative wetland change on H5N1 outbreak probability [Figure 5b]. Cumulative wetland loss had a positive association with H5N1 outbreak odds within the range of 3.1 to 153% gain. The magnitude of this association ranged between 1% (OR 1.01, 95% CI: 0.96, 1.05) and 5% (OR 1.05, 95% CI: 0.94, 1.21) increase in H5N1 outbreak odds or every 1% increase in wetland gain. On the other hand, cumulative wetland gain had a negative association with H5N1 outbreak odds over the interval of 6.4 to 100% loss and 200 to 1200% gain. The magnitude of the association in the former interval ranged between 1% (OR 0.99, 95% CI: 0.94, 1.04) and 15% (OR: 0.85, 95% CI: 0.51, 1.13) decreased odds for every one percent increase in wetland loss while the association in the latter interval ranged between 2% (OR 0.98, 95% CI: 0.67, 1.47) and 21% (OR 0.79, 95% CI: 0.16, 3.84) decreased odds for every 1% increase in wetland gain [Table 3].

Table 3: Cumulative Wetland Gain Response Intervals, 10 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-100%, -6.4%	0.85 (0.51, 1.13)	0.99 (0.94, 1.04)
3.1%, 153%	1.01 (0.96, 1.05)	1.05 (0.94, 1.21)
200%, 1200%	0.98 (0.67, 1.47)	0.79 (0.16, 3.84)

25km buffer

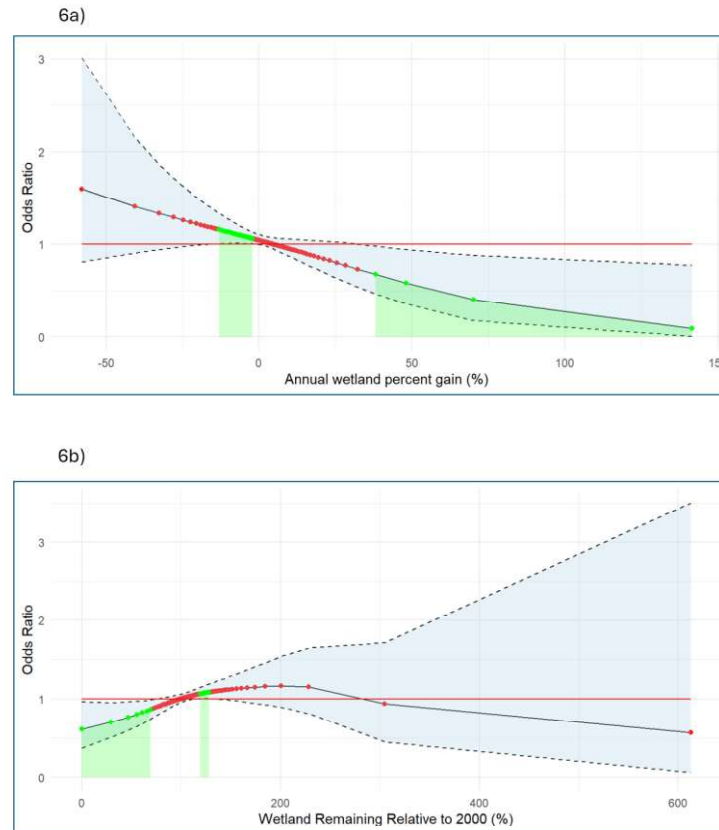


Figure 6: Exposure-response (H5N1 outbreak odds) curve, 10km buffer. Odds ratios calculated as the mean of the posterior distribution over values of wetland gain). Random walk 2 smoothing function is shown as a solid black line, with 95% credible interval bounds shaded in blue and bordered by black dotted lines. **6a):** Mean odds ratio for annual percent wetland gain; **6b):** Mean odds ratio for cumulative wetland gain between 2000 and 2026. *Red dots:* values of the exposure for which the corresponding OR is non-significant. *Green dots:* values of the exposure for which the corresponding OR is significant. *Green shading:* Intervals of the exposure for which the corresponding odds ratio is statistically significant intervals are shaded in green. *Red line:* The null odds ratio OR = 1

Results for the 25 km buffer are shown in Figure 6. The RW2 smoothing function in Figure 6a shows a continuous, approximately linear decrease in H5N1 outbreak odds with increasing wetland gain. The smoothing function for cumulative wetland gain in Figure 6b followed the same pattern as cumulative wetland gain figure in Figure 5b, where the odds ratio increased and peaked before gradually decreasing with increased wetland gain. Annual wetland change had a positive association with H5N1 outbreak odds between the interval of 57.9% loss and 4.83% gain. This association was significant in the range of 13.1% loss (OR 1.16, 95% CI: 1.01, 1.34) to 2.18% loss (OR 1.06, 95% CI: 1.01, 1.13). The magnitude of this association ranged from 6% elevated outbreak odds to 16% higher odds for every one percent increase in wetland loss within the interval [Table 4].

Annual wetland change had a negative association with H5N1 outbreak odds when annual wetland gain ranged between 5.18% to 142%. This association was statistically significant within the range of 38.1% (OR = 0.68, 95% CI: 0.47, 0.98) and 142%, (OR = 0.09,

95% CI: 0.01, 0.77) wetland gain. This indicates that an annual increase in wetland area between 38.1% and 142% is associated with a 32% to 91% decreased odds of H5N1 outbreaks for every one percent increase in wetland gain [Table 4].

Table 4: Annual Wetland Gain Significant Response Intervals, 25 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-13.1%, -2.18%	1.06 (1.01, 1.13)	1.16 (1.01, 1.34)
38.1%, 142%	0.09 (0.01, 0.77)	0.68 (0.47, 0.98)

H5N1 outbreak odds were positively associated with cumulative wetland change in the range of 0.5% loss and 128% gain (Figure 6b) between 2000-2026; this association reached statistical significance between the range of 19% (OR = 1.07 95% CI: 1.01, 1.19), and 28.2% (OR = 1.09, 95% CI: 1.01, 1.14) cumulative gain, corresponding to 7-9% increased odds over his interval per every one percent increase in wetland gain. Outbreak odds were negatively associated with cumulative wetland change outside of this interval; this association reached statistical significance between a cumulative loss of 30.9% (OR 0.86, 95% CI: 0.74, 0.99) and 100% (OR 0.61, 95% CI: 0.37, 0.97) in wetland area between 2000 and 2026. This corresponds to a 14-39% decrease in odds over this interval per every 1% increase in wetland loss [Table 5].

Table 5: Cumulative Wetland Gain Significant Response Intervals, 25 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-100%, -30.9%	0.61 (0.37, 0.97)	0.86 (0.74, 0.99)
19%, 28.2%	1.07 (1.01, 1.19)	1.09 (1.01, 1.14)

50km buffer

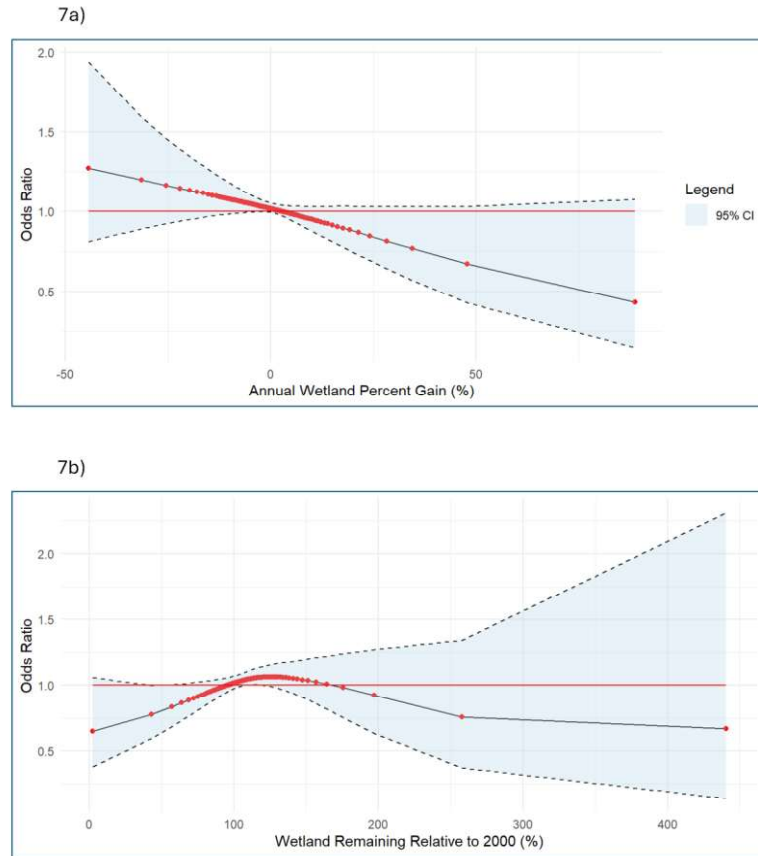


Figure 7: Exposure-response (H5N1 outbreak odds) curve, 10km buffer. Odds ratios calculated as the mean of the posterior distribution over values of wetland gain). Random walk 2 smoothing function is shown as a solid black line, with 95% credible interval bounds shaded in blue and bordered by black dotted lines. 7a: Mean odds ratio for annual percent wetland gain; 7b: Mean odds ratio for cumulative wetland gain between 2000 and 2026. *Red dots*: values of the exposure for which the corresponding OR is non-significant. *Green dots*: values of the exposure for which the corresponding OR is significant. *Green shading*: Intervals of the exposure for which the corresponding odds ratio is statistically significant intervals are shaded in green. *Red line*: The null odds ratio OR = 1

Results for the 50 km buffer are shown in Figure 7. There was no statistically significant association between annual or cumulative wetland loss and H5N1 outbreak odds in the 50 km buffer model. The RW2 smoothing function for annual wetland loss in Figure 7a demonstrated a continuous, approximately linear decrease in H5N1 outbreak probability with increasing annual wetland gain. Additionally, the smoothing function in Figure 7b demonstrated an initial increase in H5N1 outbreak odds with increasing cumulative wetland loss before decreasing for the remainder of the interval. Annual wetland change had a positive association with H5N1 outbreak odds between the interval of 44.3% loss and 1.5% gain. The magnitude of the association ranged between a 1% (OR 1.01, 95% CI: 0.98, 1.04) and 27% (OR = 1.27, 95% CI: 0.81, 1.94) increase in H5N1 odds for every 1% increase in wetland loss. There was a negative association between the interval of 3.4% gain to 88.7% gain ranging between a magnitude of 1% (OR = 0.99, 95% CI: 0.96, 1.04) and 57% (OR = 0.43, 95% CI: 0.15, 1.07) decrease in H5N1 odds for every 1% increase in wetland gain [Table 6].

Table 6: Annual Wetland Gain Significant Response Intervals, 50 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-44.3%, 1.5%	1.01 (0.98, 1.04)	1.27 (0.81, 1.95)
3.4%, 88.7%	0.43 (0.15, 1.07)	0.99 (0.96, 1.04)

Cumulative wetland change had a positive association with H5N1 outbreak odds between 4.3% loss and 64.2% gain. The magnitude of this association ranged between a 1% (OR 1.01, 95% CI: 0.96, 1.06) and 6% (OR 1.06, 95% CI: 0.98, 1.16) increase in H5N1 odds for every one percent increase in wetland gain. Cumulative wetland change had a negative association with H5N1 outbreak odds over two intervals. When cumulative wetland change ranged between 97.7 and 6.2% loss, the magnitude of the association between cumulative wetland loss and H5N1 outbreak odds ranged between a 1% (OR 0.99, 95% CI: 0.94, 1.05) and 35% (OR 0.65, 95% CI: 0.38, 1.06) decrease in H5N1 outbreak odds for every one percent increase in wetland loss. When wetland gain was between 75.5 and 340.3%, the odds for H5N1 outbreak occurrence decreased between 2% (OR = 0.98, 95% CI: 0.75, 1.23) and 33% (OR = 0.67, 95% CI: 0.14, 2.31) for every one percent increase in wetland gain [Table 7].

Table 7: Cumulative Wetland Gain Response Intervals, 10 Km Model

Wetland gain interval (min, max)	Minimum OR in interval (95% CI)	Maximum OR in interval (95% CI)
-97.7%, -6.2%	0.65 (0.38, 1.06)	0.99 (0.94, 1.05)
-4.3%, 64.2%	1.01 (0.96, 1.06)	1.06(0.98, 1.16)
75.5%, 340.4%	0.67 (0.14, 2.31)	0.98 (0.75, 1.23)

The distribution of annual wetland change over time for all buffer zones is plotted in Figures 8-10. Figure 8 shows considerable more spread in mean wetland gain than Figures 9 and 10. This difference in spread is also reflected in the error bars for mean annual wetland gain being greater at the 10 km buffer distance compared to the 25 and 50 km buffer distances. Additionally, the annual wetland loss for many buffer zones lie several standard deviations from the mean.

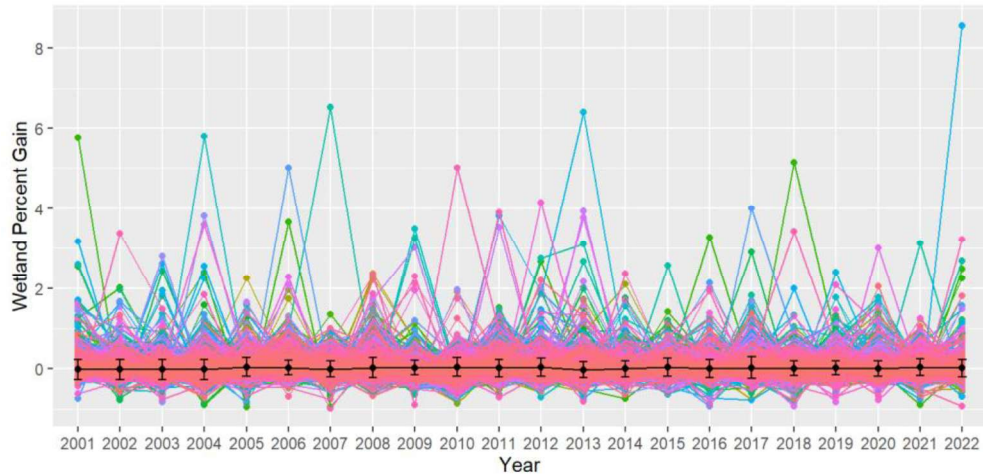


Figure 8: Plot of annual wetland gain over time for cases and controls, 10 km model. Dots represent values of annual wetland gain for buffer zones calculated between 2000-2001 until 2021-2022. Individual buffer zones are color coded. Mean wetland gain averaged over all buffer zones is over time is shown as black dots joined by a black line. Error bars are shown in black as one standard deviations from the mean. Points where annual percent gain was greater than 10 have been removed for visualization purposes (n = 10).

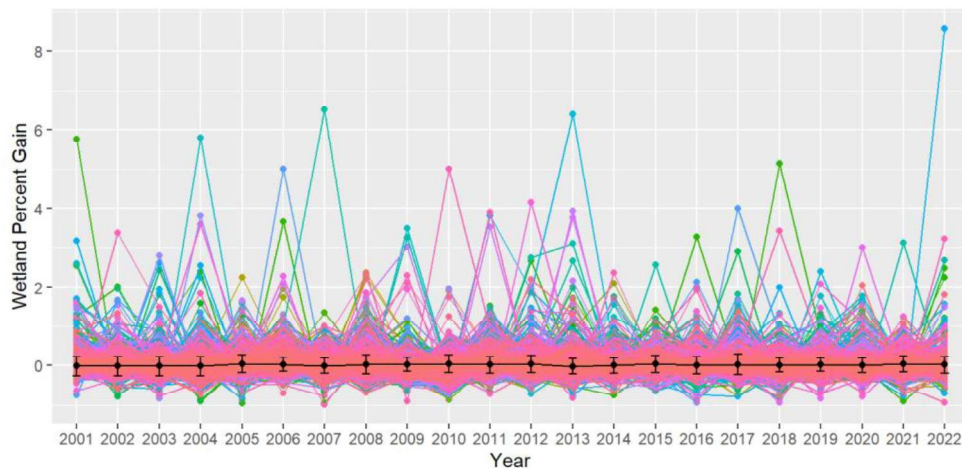


Figure 9: Plot of annual wetland gain over time for cases and controls, 25 km model. Dots represent values of annual wetland gain for buffer zones calculated between 2000-2001 until 2021-2022. Individual buffer zones are color coded. Mean wetland gain averaged over all buffer zones is over time is shown as black dots joined by a black line. Error bars are shown in black signifying one standard deviation from the mean. Points where annual percent gain was greater than 10 have been removed for visualization purposes (n = 9)

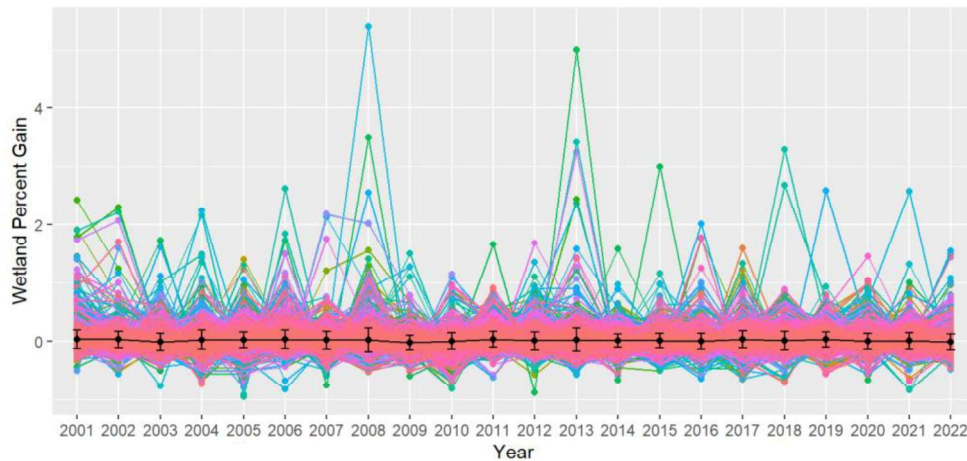


Figure 10: Plot of annual wetland gain over time for cases and controls, 50 km model. Dots represent values of annual wetland gain for buffer zones calculated between 2000-2001 until 2021-2022. Individual buffer zones are color coded. Mean wetland gain averaged over all buffer zones is over time is shown as black dots joined by a black line. Error bars are shown in black signifying one standard deviation from the mean.

Discussion:

In this study, we observed a significant association between wetland habitat loss and H5N1 outbreak occurrence after adjusting for major confounders; importantly the nature of this association differed with choice of buffer size. The findings of our 10 km buffer model were consistent with our hypothesis that decreasing wetland availability increases the odds of virus transmission. Namely, annual wetland loss of up to 16.4% was associated with up to 13% increased odds of H5N1 outbreak occurrence for every one percent increase in wetland loss. Furthermore, annual gains in wetland area between 37.6 to 116% were significantly associated with a 22% to 57% lower odds of H5N1 outbreaks for every one percent increase in wetland gain. These findings persisted in our 25 km model where we observed that wetland loss of up to 13.1% was associated with up to 16% increased odds for H5N1 outbreak occurrence for every one percent increase in wetland loss. Annual gains in wetland area between 38.1 to 141.5% were also associated with 32% to 91% lower outbreak odds for every one percent increase in wetland gain. However, there was no significant association between annual wetland loss and outbreak odds for the 50 km buffer model. Only the 25 km buffer model showed a significant association between cumulative wetland change and H5N1 outbreak odds. We found that H5N1 outbreak odds were reduced by 14 to 39% for every one percent increase in wetland loss when cumulative wetland loss between 2000 and 2026 ranged between 31 to 100%. This indicates reduced outbreak odds as wetlands vanish. Furthermore, when there was a cumulative increase in wetland habitat between 19 to 28.2%, the outbreak odds were elevated by 7 to 9% per every one percent increase in wetland gain. Both the 10 km and 50 km models showed that cumulative wetland loss was associated with decreased outbreak odds, but these associations were not statistically significant at either distance.

Altogether, our results indicate that annual wetland loss is associated with increased H5N1 outbreak odds within 10 km of a location. Cumulative wetland loss at this distance,

however, is associated with decreased outbreak odds but this association is not statistically significant. Our results also show that wetland loss within 25 km of a location is also associated with increased disease odds, but these results are directly contradicted by the finding that cumulative wetland loss within this same distance is significantly associated with decreased odds of H5N1 outbreaks. The 50 km buffer model also demonstrated contradictory findings where annual wetland loss was associated with increased H5N1 outbreak odds while cumulative wetland loss was associated with decreased odds, but neither association was statistically significant.

Our expectation was that if annual wetland loss was associated with increased H5N1 outbreak odds for any buffer zone model, cumulative wetland loss would follow suit. Instead, we saw that annual wetland loss was associated with increased H5N1 odds while cumulative wetland loss was associated with decreased outbreak odds at all three buffer zones. One explanation for these contradictory findings could be that long-term wetland loss reduces migratory waterfowl populations at stopover sites over time²². Wetland loss can cause a reduction of food at roosting and stopover sites or destroy them altogether, reducing their suitability for migratory waterfowl^{42,43}. When primary food sources become unavailable, migratory waterfowl turn to alternate stopover and roosting sites with better resource access⁴⁴. Reduced food availability along migration routes is also associated with reduced reproductive success, and in cases when migrating waterfowl cannot find alternative roosting and stopover sites, population collapse^{13,42}. As such, these factors suggest that the decrease in H5N1 outbreak odds we observed with cumulative wetland loss could be due to decreased waterfowl visitation of those sites driven by shifts to alternate roosting and stopover sites and decreasing waterfowl population density between 2000 and 2026. This could consequently lead to decreased interactions in those areas between domestic poultry and wild waterfowl. However, to confirm this theory, we would need to track waterfowl density in these locations over time.

Another reason we see a conflicting trend in outbreak odds between annual and cumulative wetland loss could be the different ways in which long and short-term changes affect avian influenza ecology⁴⁵. The association between annual wetland loss and H5N1 outbreak odds is the function of how wetland loss over the course of a year impacts H5N1 odds. Vandegrift *et al.*, (2020) suggest that the short-term effect of such wetland loss results in increased waterfowl aggregation at remaining stopover, breeding, and wintering sites which increases the frequency of contacts between wild birds and domestic poultry⁴⁵. On the other hand, the association between cumulative wetland loss and H5N1 odds in our study measures a long-term process. Vandegrift *et al.*, (2020) also suggests that a long-term effect of wetland loss is the reduction of wetland-dependent waterfowl in the area which is consistent with the assertions of Newton (2004) and Xu *et al.*, (2019) that wetland loss is associated with diminishing waterfowl population in wetlands over time^{22,42,45}. As such, changes in contact frequency between migratory waterfowl and domestic poultry attributed to annual and cumulative wetland loss could potentially explain our contradictory results.

Something else to consider in these results is the degree to which increased H5N1 outbreak odds are actually due to wetland loss. We have theorized that wetland degradation increases H5N1 odds by pushing migratory waterfowl to forage for food on farms and crop fields to meet their metabolic needs during short-term stop overs and longer-term roosting. Johnson *et al.*, (2014) studied foraging flights taken by ducks and geese from wintering sites and found that

the average foraging flight is 7.4 km (SD = 7.2) for geese and 5.1 km (SD = 4.4) for ducks⁴⁶. This suggests that the average distance traveled by wintering geese and ducks tends to be less than 10 km on average. As such, almost the entirety of our 10 km buffer zones would be within foraging flight distance of any birds that were roosting within those buffer zones. This would make it plausible that viral spread could be a consequence of wetland loss pushing wintering waterfowl to forage in farms or cropland away from their roosting sites. It is more difficult to tell whether this is the case for the 25 and 50 km buffer zones. For example, wetland loss 40 km from an outbreak is considerably less likely to increase H5N1 outbreak odds by pushing birds to forage outside of wetlands than wetland loss within 10 km. This, in turn, reduces the assumptions we can make about the mechanism through which wetland loss affects H5N1 outbreak odds at distances exceeding 10 km.

Our results also suggest that H5N1 outbreak odds at a location can be mitigated by increasing wetland habitat in the immediate area. We also found evidence at the 10 and 25 km buffer distance that annually increasing wetland habitat around a location can mitigate outbreak odds seen by the significant reduction in H5N1 outbreak odds that accompanied wetland gain at both distances. This makes sense, given that wetlands increasing in size would be expected to have good food availability, reducing the need and frequency for migratory waterfowl to take foraging flights that could result in contact with domestic poultry or bridge hosts⁴⁷.

One limitation of this study arises from the use of satellite data. The authors of the GLC_FCS30D database indicate that there is variability in this data and estimate that the classification in this dataset is 80.88% accurate³³. This variability derives from a number of factors. For one, satellite imagery may not be 100% accurate due to cloud cover when images were taken and issues like miscalibrated sensors and atmospheric interference may also influence image quality. It is also likely that some degree of change identified in any remote sensing data over time is reflective of improvements in sensing technology and mapping over that period of time. Additionally, wetland habitats classification can vary between sources which limit the degree to which analyses using this dataset can be compared with analyses done with other data. Wetland habitats in this study were classified by the authors of GLC_FCS30D, and this classification may differ from other sources³³. Altogether, the influence that these factors have on image quality is a reminder that this analysis is an *approximation* and our best estimate at mapping spatiotemporal trends given the technology and circumstances that affect the quality of the images used for this analysis.

Another potential limitation arises from control selection. Control selection was done entirely at random as opposed to selecting farms or cropland as control sites. This means that control sites could have been devoid of poultry without capacity for H5N1 poultry outbreaks. Any future analyses using this data will be performed using a new set of control sites where possible sites will be confined to land classified as cropland by the GLC_FCS30D dataset. Residual confounding is another potential source of bias. While distance to the nearest wetland was considered as a confounder, distance to the nearest cropland was not included in our model. One reason this was not added to our model was due to overfitting concerns since our model already had 7 variables. However, it is possible that by excluding this variable we did not adjust for a potential source of confounding as proximity to farmland can be linked to both wetland loss and H5N1 outcome odds, given the historical conversion of wetlands to cropland and the association and the findings in Cullen *et al.*, (2025) that spatiotemporal overlap between wild

waterfowl and poultry farms was associated with elevated HPAI risk^{18,48}. The assumptions used to impute data for missing covariates are also another potentially limiting factor for this study. We imputed annual wetland and cropland change data beyond the temporal extent of the GLC_FCS30D dataset (2023-2026) by calculating the average change in both variables for each buffer zone for all years between 2000 and 2022. This single average was used as an estimate for annual wetland change in 2023 to 2026. A consequence of assuming a constant rate of change between 2023 to 2026 is that we would not have been able to capture non-linear trends in wetland and cropland change between 2023 to 2026. It can also be noted, however, from Figures 8-10, that many response values for annual wetland loss lie several standard deviations from the mean. This suggests that using the mean of annual wetland loss between 2000 to 2026 for each buffer zone to impute values for 2023 to 2026 likely did not accurately capture the variation associated with annual changes to wetland loss. For future studies, we plan to use data sources with greater temporal range to avoid having to perform imputation.

Lastly, another limitation is the potential for underreporting of H5N1 outbreaks. The EMPRES-i database relies on data reporting from local sources⁶. As such, H5N1 cases that were not reported to authorities would not be captured in the EMPRES-i database. Backyard poultry operations are vulnerable to reporting bias since accurate reporting relies on farmers having a thorough understanding of H5N1 signs and symptoms in domestic poultry. However, a survey of 638 backyard flock owners in the United States showed that only a third of respondents were able to correctly identify all signs of avian influenza in birds⁴⁹. This suggests that many poultry flock owners lack an understanding of H5N1 symptoms and may not be able to identify and subsequently report H5N1 cases. As such, it should be assumed that the EMPRES-i dataset used for this analysis did not capture all H5N1 outbreaks between 2022 to 2026.

Conclusion:

Our findings indicate that changes in wetland habitat over time are associated with H5N1 outbreak odds in domestic poultry in the United States. We found that annual wetland loss of up to 25 km is significantly associated with elevated odds of H5N1 outbreak occurrence which was consistent with our expectations. The literature provides a possible explanation for why this could have occurred. It is possible that wetland loss and subsequent degradation of stopover, breeding, and winterings sites could have reduced food available to migratory waterfowl at these locations and pulled them to forage in agricultural land, where they would have had access to grain, seeds, and other food sources^{10,25,27}. It is possible that at these sites, wild waterfowl infected with H5N1 spread the virus to domestic poultry either directly, through bridge hosts, or through environmental contamination via fecal matter^{3,11}. Since the upper limit of foraging distance for ducks and geese is approximately 10 km, it is possible that the association we observed within our 10 km buffer model could be the result of this mechanism⁴⁶. Our finding that cumulative wetland loss tended to be associated with reduced H5N1 outbreak odds was the opposite of what we expected. However, this can be explained by long-term wetland loss reducing waterfowl population in the region over time as migratory birds turn to alternate roosting and stopover sites or die out altogether^{22,42}. On the other hand, annual wetland loss can increase waterfowl density at productive sites in the vicinity of the area, increasing viral

circulation within migratory populations and contact between infected waterfowl and domestic poultry^{22,31}. These differences in how year-to-year and long-term wetland loss affect H5N1 transmission could be why annual wetland loss was associated with increased H5N1 outbreak odds while cumulative wetland loss was associated with decreased odds. However, we would need longitudinal waterfowl density data to verify this.

Another key finding is that annual increases in wetland habitat are associated with decreasing disease odds up to 25 km. This trend also provides evidence that the association between annual wetland habitat change and H5N1 outbreak odds is bidirectional. While we show that wetland loss can increase odds for future disease outbreaks, we also provide evidence that wetland restoration could have a protective effect that reduces H5N1 odds to domestic poultry on farms within 10 km of a given location. This finding has implications for conservation, as if wetland restoration projects in the vicinity of commercial and backyard poultry operations could reduce the odds of H5N1 infecting domestic poultry flocks. More research about how anthropogenic change affects disease odds over time is critical to preventing future disease outbreaks, and we recommend that future studies continue using satellite data to further understand how human activity affects the ecology of disease spillover and transmission.

References:

1. Youk S, Torchetti MK, Lantz K, et al. H5N1 highly pathogenic avian influenza clade 2.3.4.4b in wild and domestic birds: Introductions into the United States and reassortments, December 2021–April 2022. *Virology*. 2023;587:109860. doi:10.1016/j.virol.2023.109860
2. Lycett SJ, Duchatel F, Digard P. A brief history of bird flu. *Philos Trans R Soc Lond B Biol Sci*. 2019;374(1775):20180257. doi:10.1098/rstb.2018.0257
3. Tripathi AK, Sendor AB, Sapra A. Avian Influenza. In: *StatPearls*. StatPearls Publishing; 2026. Accessed August 13, 2026. <http://www.ncbi.nlm.nih.gov/books/NBK553072/>
4. Blais-Savoie J, Halajian E, Nirmalarajah K, et al. Examining the Threat of H5N1 Highly Pathogenic Avian Influenza to Human Health. *CHEST*. 2026;169(4):947-957. doi:10.1016/j.chest.2025.10.030
5. Palù G, Roggero PF, Calistri A. Could H5N1 bird flu virus be the cause of the next human pandemic? *Front Microbiol*. 2024;15:1477738. doi:10.3389/fmicb.2024.1477738
6. Food and Agricultural Organization of the United Nations. EMPRES-i +. Published online February 6, 2026. Accessed July 7, 2026. <https://empres-i.apps.fao.org/diseases>
7. World Organization for Animal Health. WAHIS: World Animal Health Information System. Published online October 11, 2025. <https://wahis.woah.org/#/home>
8. Lin TH, Zhu X, Wang S, et al. A single mutation in bovine influenza H5N1 hemagglutinin switches specificity to human receptors. *Science*. 2024;386(6726):1128-1134. doi:10.1126/science.adt0180

9. Man W, Du L, Liu Y, et al. Evolution of H5N1 Cross-Species Transmission: Adaptive Mutations Driving Avian-to-Human Infection. *Adv Genet.* 2026;7(1):e00051. doi:10.1002/ggn2.202500051
10. Martelli L, Fornasiero D, Scarton F, et al. Study of the Interface between Wild Bird Populations and Poultry and Their Potential Role in the Spread of Avian Influenza. *Microorganisms.* 2023;11(10):2601. doi:10.3390/microorganisms11102601
11. Blagodatski A, Trutneva K, Glazova O, et al. Avian Influenza in Wild Birds and Poultry: Dissemination Pathways, Monitoring Methods, and Virus Ecology. *Pathog Basel Switz.* 2021;10(5):630. doi:10.3390/pathogens10050630
12. Lee K, Yu D, Martínez-López B, et al. Fine-scale tracking of wild waterfowl and their impact on highly pathogenic avian influenza outbreaks in the Republic of Korea, 2014-2015. *Sci Rep.* 2020;10(1):18631. doi:10.1038/s41598-020-75698-y
13. Ballard DC, Jones OE, Janke AK. Factors Affecting Wetland Use by Spring Migrating Ducks in the Southern Prairie Pothole Region. *J Wildl Manag.* 2021;85(7):1490-1506. doi:10.1002/jwmg.22096
14. Lang MW, Ingebritsen JC, Griffin RK. 2019 Wetlands Status and Trends Report | U.S. Fish & Wildlife Service. April 1, 2024. Accessed July 7, 2026. <https://www.fws.gov/project/2019-wetlands-status-and-trends-report>
15. Nelms KD, Ballinger B, Boyles A. Wetland Management for Waterfowl Handbook. Published online 2007. <https://www.nrcs.usda.gov/sites/default/files/2023-08/NRCS-Wetland-Management-for-Waterfowl-Handbook.pdf>
16. Blount JD, Horns JJ, Kittelberger KD, Neate-Clegg MHC, Şekercioğlu ÇH. Avian Use of Agricultural Areas as Migration Stopover Sites: A Review of Crop Management Practices and Ecological Correlates. *Front Ecol Evol.* 2021;9:650641. doi:10.3389/fevo.2021.650641
17. Davis BJ, Boudreau MR, Peterson TG, Kaminsky RM, Colvin ME. Wintering Waterfowl Use of Wetlands in Delta National Forest, Mississippi. *J Southeast Assoc Fish Wildl Agencies.* 2022;9:96-104.
18. Olsson L, Barbosa H, Bhadwal S, et al. *Land Degradation*. United Nations Office for Disaster Risk Reduction.
19. Bettigole C, McClure M, Wilson A, Kolodney S, Kazanski C, Gennet S. Mapping Grazing Lands for the Conterminous United States. *Rangel Ecol Manag.* 2026;107:15-27. doi:10.1016/j.rama.2026.03.003
20. Wilen BO, Frayer WE. Status and trends of U.S. wetlands and deepwater habitats. *For Ecol Manag.* 1990;33-34:181-192. doi:10.1016/0378-1127(90)90192-E
21. Apogee Research, Inc. *Quantifying the Impacts of Road Construction on Wetlands Loss : Preliminary Analysis*. United States Department of Transportation; 1997:17. <https://rosap.ntl.bts.gov/view/dot/13617>

22. Newton I. Population limitation in migrants. *Ibis*. 2004;146(2):197-226. doi:10.1111/j.1474-919X.2004.00293.x
23. Guo F, Buler JJ, Smolinsky JA, Wilcove DS. Seasonal patterns and protection status of stopover hotspots for migratory landbirds in the eastern United States. *Curr Biol*. 2024;34(2):235-244.e3. doi:10.1016/j.cub.2023.11.033
24. Gaidet N, Caron A, Cappelle J, et al. Understanding the ecological drivers of avian influenza virus infection in wildfowl: a continental-scale study across Africa. *Proc R Soc B Biol Sci*. 2012;279(1731):1131-1141. doi:10.1098/rspb.2011.1417
25. McDuie F, Matchett EL, Prosser DJ, et al. Pathways for avian influenza virus spread: GPS reveals wild waterfowl in commercial livestock facilities and connectivity with the natural wetland landscape. *Transbound Emerg Dis*. 2022;69(5):2898-2912. doi:10.1111/tbed.14445
26. Pearse AT, Krapu GL, Cox RR. Comparative Spring-Staging Ecology of Sympatric Arctic-Nesting Geese in South-Central Nebraska. *Am Midl Nat*. 2013;169(2):371-381. doi:10.1674/0003-0031-169.2.371
27. Sánchez-Cano A, Camacho MC, Ramiro Y, Cardona-Cabrera T, Höfle U. Seasonal changes in bird communities on poultry farms and house sparrow—wild bird contacts revealed by camera trapping. *Front Vet Sci*. 2024;11:1369779. doi:10.3389/fvets.2024.1369779
28. Kaplan BS, Webby RJ. The avian and mammalian host range of highly pathogenic avian H5N1 influenza. *Virus Res*. 2013;178(1):3-11. doi:10.1016/j.virusres.2013.09.004
29. Damodaran L, Jaeger AS, Moncla LH. Ecology and spread of the North American H5N1 epizootic. *Nature*. 2026;649(8096):432-441. doi:10.1038/s41586-025-09737-x
30. Wu T, Perrings C, Shang C, et al. Protection of wetlands as a strategy for reducing the spread of avian influenza from migratory waterfowl. *Ambio*. 2020;49(4):939-949. doi:10.1007/s13280-019-01238-2
31. Cappelle J, Gaidet N, Iverson SA, et al. Characterizing the interface between wild ducks and poultry to evaluate the potential of transmission of avian pathogens. *Int J Health Geogr*. 2011;10(1):60. doi:10.1186/1476-072X-10-60
32. Green AL, Branan M, Fields VL, et al. Investigation of risk factors for introduction of highly pathogenic avian influenza H5N1 virus onto table egg farms in the United States, 2022: a case–control study. *Front Vet Sci*. 2023;10:1229008. doi:10.3389/fvets.2023.1229008
33. Zhang X, Zhao T, Xu H, et al. GLC_FCS30D: the first global 30 m land-cover dynamics monitoring product with a fine classification system for the period from 1985 to 2022 generated using dense-time-series Landsat imagery and the continuous change-detection method. *Earth Syst Sci Data*. 2024;16(3):1353-1381. doi:10.5194/essd-16-1353-2024
34. Fang LQ, De Vlas SJ, Liang S, et al. Environmental Factors Contributing to the Spread of H5N1 Avian Influenza in Mainland China. Montgomery JM, ed. *PLoS ONE*. 2008;3(5):e2268. doi:10.1371/journal.pone.0002268

35. US Census Bureau. TIGER/Line Shapefiles. Census.gov. Accessed July 8, 2026.
<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>
36. U.S. Geological Survey (USGS) Gap Analysis Project (GAP). Protected Areas Database of the United States (PAD-US) 3.0 (ver. 2.0, March 2023). Published online March 20, 2023.
doi:10.5066/P9Q9LQ4B
37. Woods S. *Wetlands in Peril: How Agriculture Damages Critical Ecosystems, Increasing Flood Risk in the Upper Midwest*. Union of Concerned Scientists; 2024.
doi:10.47923/2024.15677
38. Gilbert M, Prosser DJ, Zhang G, et al. Could Changes in the Agricultural Landscape of Northeastern China Have Influenced the Long-Distance Transmission of Highly Pathogenic Avian Influenza H5Nx Viruses? *Front Vet Sci*. 2017;4:225. doi:10.3389/fvets.2017.00225
39. Mateus-Anzola J, Gaytan-Cruz L, Espinosa-García AC, Martínez-López B, Ojeda-Flores R. Risk for Waterborne Transmission and Environmental Persistence of Avian Influenza Virus in a Wildlife/Domestic Interface in Mexico. *Food Environ Virol*. 2024;16(4):458-469.
doi:10.1007/s12560-024-09608-0
40. Walsh MG, Mor SM, Hossain S. Highly Pathogenic Avian Influenza (H5N1) Landscape Suitability Varies by Wetland Habitats and the Degree of Interface between Wild Waterfowl and Poultry in India. *Viruses*. 2020;12(11):1290. doi:10.3390/v12111290
41. Chanda MM, Shivachandra SB, Mishra A, et al. Unique duck rearing practice in irrigated rice paddy fields driving recurrent H5N1 avian influenza outbreaks in two districts of Kerala, India. *Epidemiol Infect*. 2025;153:e17. doi:10.1017/S0950268824001882
42. Xu Y, Si Y, Yin S, et al. Species-dependent effects of habitat degradation in relation to seasonal distribution of migratory waterfowl in the East Asian–Australasian Flyway. *Landsc Ecol*. 2019;34(2):243-257. doi:10.1007/s10980-018-00767-7
43. Klaassen M, Hoyer BJ, Nolet BA, Buttemer WA. Ecophysiology of avian migration in the face of current global hazards. *Philos Trans R Soc B Biol Sci*. 2012;367(1596):1719-1732.
doi:10.1098/rstb.2012.0008
44. Yin S, Zhang C, Teitelbaum CS, et al. Landscape changes elevate the risk of avian influenza virus diversification and emergence in the East Asian–Australasian Flyway. *Proc Natl Acad Sci*. 2025;122(34):e2503427122. doi:10.1073/pnas.2503427122
45. Vandegrift KJ, Sokolow SH, Daszak P, Kilpatrick AM. Ecology of avian influenza viruses in a changing world. *Ann N Y Acad Sci*. 2010;1195(1):113-128. doi:10.1111/j.1749-6632.2010.05451.x
46. Johnson WP, Schmidt PM, Taylor DP. Foraging flight distances of wintering ducks and geese: a review. *Avian Conserv Ecol*. 2014;9(2):art2. doi:10.5751/ACE-00683-090202
47. Kapan DD, Bennett SN, Ellis BN, et al. Avian Influenza (H5N1) and the Evolutionary and Social Ecology of Infectious Disease Emergence. *EcoHealth*. 2006;3(3):187-194.
doi:10.1007/s10393-006-0044-6

48. Cullen JA, Mastro NM, Sullivan JD, et al. Spatiotemporal Overlap of Mallards With Poultry Farms Is Associated With Greater Risk of Avian Influenza Wild Bird Spillover Events. *Ecol Evol*. 2025;15(10):e72221. doi:10.1002/ece3.72221
49. Rolfes MA, Bauck L, Lipton BA, et al. Knowledge, Attitudes, and Practices Regarding Avian Influenza Among Owners of Backyard Flocks — United States, July–December 2025. *MMWR Morb Mortal Wkly Rep*. 2026;75(18):234-239. doi:10.15585/mmwr.mm7518a2