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Research article

Potential use of poultry farms by wild waterfowl in California's Central Valley varies across space, times of day, and species: implications for influenza transmission risk

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Interactions between wildlife and livestock can lead to cross-species disease transmission, which incurs economic costs and threatens wildlife conservation. Wild waterfowl are natural hosts of avian influenza viruses (AIVs), are often abundant near poultry farms, and have been linked to outbreaks of AIVs in poultry. Interspecific and seasonal variation in waterfowl movement and habitat use means that the risk of disease transmission between wild birds and poultry inevitably varies across species, space, and time. Here, we used GPS telemetry data from 10 waterfowl species in and near California's Central Valley, a region where both wild waterfowl and domestic poultry are abundant, to study selection of poultry farms by waterfowl across diel, seasonal, and annual cycles. We found that waterfowl selected for wetlands, open water, protected areas, and croplands, which meant that they generally avoided habitats that were likely to be used for poultry farming. These selection patterns were linked to species' ecology and diel behavioral patterns, such that avoidance of poultry habitats was stronger for local or partial migrants than for long-distance migrants, and stronger during daytime than at night. We then combined these habitat selection results with data on poultry farm locations to map risk of waterfowl–poultry contact across the Central Valley. Average selection strength at poultry farms was low, suggesting that current placement of poultry farms is generally effective for limiting risk of contact with wild birds. When we combined these habitat selection results with data on species' abundances and AIV infection prevalence, we found dramatic variation in potential AIV transmission risk among species. These results could be used to prioritize surveillance and biosecurity efforts for regions and times of relatively high risk. More generally,

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these results highlight that fine-scale movement data can help identify interspecific, seasonal, and diel patterns in animal behaviors that affect wildlife and poultry health.

Keywords: avian influenza, habitat selection, poultry, spillover, step-selection, waterfowl, wildlife–agriculture interface

Introduction

Agricultural development and urbanization are increasing the frequency of interactions among wildlife, domestic animals, and people, which can lead to cross-species disease transmission and the emergence of infectious diseases in wildlife, livestock, and humans (Bradley and Altizer 2007, Hassell et al. 2017). Some wildlife–livestock–human interfaces are more likely than others to promote cross-species disease transmission (Hassell et al. 2017). For instance, systems where wildlife and livestock are closely related are more likely to be points of transmission than ones where livestock are taxonomically distinct from wildlife (e.g. bovine tuberculosis in wild ungulates and domestic cattle, Renwick et al. 2007, Olival et al. 2017). In addition, viral and bacterial pathogens are more likely to cross species boundaries than helminth, fungal, or protozoan parasites, possibly because they have higher mutation rates (Jones et al. 2008). The frequency of interactions between wildlife and livestock also depends on habitat selection by wildlife (Hahn et al. 2014). Wildlife species, populations, or individuals that tolerate (or are attracted to) urban and agricultural landscapes are more likely to contact humans and domestic animals than are those that avoid these developed landscapes (Rayl et al. 2021).

Cross-species disease transmission is important for the ecology of avian influenza viruses (AIVs). Wild ducks, geese, and swans (i.e. waterfowl) are natural reservoirs of low pathogenic avian influenza (LPAI) and AIVs frequently circulate among multiple waterfowl species (Olsen et al. 2006, Hicks et al. 2022). When introduced to domestic poultry populations, LPAI can mutate into highly pathogenic avian influenza (HPAI; Capua and Alexander 2006, Hill and Runstadler 2016), which can cause significant morbidity and mortality, sometimes affecting tens of millions of birds (Ramos et al. 2017, Harvey et al. 2023, Lean et al. 2023). Genetic evidence shows that outbreaks of HPAI in wild birds and poultry result from transmission between wild birds and poultry, as well as from transmission within wild bird populations or among poultry farms (Verhagen et al. 2021, King et al. 2022). The ongoing global outbreaks of HPAI are threatening sensitive wild bird species (Harvey et al. 2023, Lean et al. 2023) and HPAI occasionally infects wild mammals and humans (Lycett et al. 2019, Chauhan and Gordon 2021). Because of the importance of waterfowl–poultry contact for HPAI transmission, characterizing the probability and nature of this contact is important for informing biosecurity and wildlife management, with implications for wild bird, mammal, and poultry health.

Habitat use and local abundances of wild waterfowl have been linked to AIV outbreaks in both poultry

(Humphreys et al. 2020, Lee et al. 2020, Hill et al. 2021) and wild waterfowl (Gaidet et al. 2012, Gorsich et al. 2021). Waterfowl sometimes inhabit areas adjacent to poultry farms, indicating a viable pathway for direct or indirect AIV transmission between wild birds and poultry (Velkers et al. 2021, McDuire et al. 2022). The risk of cross-species transmission of AIVs should therefore be higher when wild waterfowl travel near poultry farms. Accordingly, estimates of AIV transmission risk have drawn on data on wild bird abundance (Prosser et al. 2016a), but are often based on abundance estimates at moderate to coarse spatial scales (e.g. 1–30 km², Prosser et al. 2016a), which provides an important foundation for risk assessments but does not account for small-scale variation in habitat conditions. In addition, many studies of waterfowl–poultry interactions have either ignored differences between wild bird species or have focused on a single species (Humphreys et al. 2021). However, because viral prevalence (Garamszegi and Møller 2007, Hill et al. 2010, Bianchini et al. 2021, Kent et al. 2022), susceptibility to influenza (Brown et al. 2006), habitat use (Isola et al. 2000), and movement patterns (McDuire et al. 2019) differ among species and functional groups, the risk of influenza transmission between wild birds and poultry will also vary across taxa (Hill et al. 2022). Therefore, it is important to study patterns of potential wild bird–poultry contact across multiple taxa.

California is known for both its agricultural production and its density and diversity of waterfowl. The Central Valley of California is a hotspot for overwintering migratory waterfowl, many of which use agricultural fields as habitat (Gilmer et al. 1982), and where cross-species transmission of LPAIVs among wild waterfowl is common (Hill et al. 2012). This use of agricultural areas by waterfowl provides opportunities for creating multifunctional landscapes for agriculture and conservation (Plieninger et al. 2012), but also increases the risk of AIV transmission at the wildlife–poultry and wildlife–agriculture interfaces (Belkhiria et al. 2016). Wild waterfowl have been observed at and near livestock facilities in California (McDuire et al. 2022) and waterfowl abundance tends to peak near Central Valley poultry facilities in mid-winter (Acosta et al. 2021). Several outbreaks of HPAI occurred in both wild birds and poultry in California in 2022 (USDA APHIS 2022a, b), but the sources of each outbreak are not yet known.

Here, we used high-resolution tracking data from 10 waterfowl species to analyze selection of poultry farm habitats in California across space, seasons, and species. We then used these results to calculate spatially and temporally explicit estimates of wild bird selection for poultry farms in the Central Valley. We expected that birds would generally select

for natural habitats (e.g. wetlands, open water) and agricultural forage (i.e. rice fields) over poultry habitats, and that variation in selection across seasons, species, and times of day would translate to inter-specific and temporal variation in the risk of waterfowl–poultry contact.

Material and methods

Wild bird telemetry

We used GPS tracking data to measure habitat selection of wild waterfowl. Species included in this study were two species of goose: greater white fronted goose (Pacific: *Anser albifrons sponosa* and tule: *Anser albifrons elgasi*) and lesser snow goose *Chen caerulescens*; one diving duck species: canvasback *Aythya valisineria*; and seven dabbling duck species: northern pintail *Anas acuta*, mallard *A. platyrhynchos*, green-winged teal *A. carolinensis*, cinnamon teal *Spatula cyanoptera*, northern shoveler *S. clypeata*, gadwall *Mareca strepera* and American wigeon *M. americana*. Geese, canvasback, northern pintail and American wigeon are long-distance migrants; the other dabbling duck species are partial or local migrants, with at least some GPS-tracked individuals remaining in California over summer to breed and molt.

Adult birds were captured and fitted with GPS transmitters at multiple locations and during multiple seasons in the Central Valley and the San Francisco Bay Estuary between 2015 and 2020. GPS transmitters on geese and dabbling ducks were programmed to provide locations every 30 min, unless battery levels were low, in which case they provided locations every 1–12 h. Implanted GPS transmitters on canvasbacks were programmed to provide locations every 3 h. For more detail on capture and marking, Supporting information, [McDuie et al. \(2019\)](#), and [Teitelbaum et al. \(2023a\)](#).

Poultry and land cover data

We gathered data on the spatial distribution of poultry farms in California from the farm location and agricultural production simulator (FLAPS), which provides a surface depicting the probability of poultry farm occurrence (hereafter ‘poultry habitat’) at 100 m resolution for the contiguous USA ([Burdett et al. 2015](#), [Patyk et al. 2020](#)). Values, which range from 0 to 1, represent the relative suitability of a given location for poultry farming (Supporting information) based on slope and distance to roads, croplands, water, urban land cover and open areas ([Patyk et al. 2020](#)). FLAPS masks water bodies (i.e. they are provided as missing values), so we imputed zeroes for these areas, under the assumption that poultry farms are not located in open water.

To understand how other habitat characteristics influence waterfowl use of poultry habitats, we also gathered data on land cover variables that might affect waterfowl habitat use: herbaceous wetlands, publicly owned lands, open water, and rice (Supporting information). Wetland and open water data were derived from the National Land Cover Database 2019

([Dewitz and US Geological Survey 2021](#)). Public lands data were derived from Protected Areas Database of the United States (PAD-US) database ver. 2.1 ([US Geological Survey \(USGS\) Gap Analysis Project \(GAP\) 2020](#)); we excluded lands used for extractive purposes (e.g. mines) because we aimed to represent low human disturbance with this layer. Rice data were derived from the US Department of Agriculture’s Cropland Data Layer (CDL) ([USDA National Agricultural Statistics Service 2021](#)). Because rice cover varies significantly from year to year, we used annual data from the CDL (2015–2020); all other layers were static because they vary less year to year than rice and because other data sets were available only at multi-annual temporal resolutions.

Modeling selection for poultry habitats

We used step-selection functions (SSFs; [Fortin et al. 2005](#), [Thurfjell et al. 2014](#)) to analyze relationships between habitat variables and waterfowl movements. Like resource selection functions, SSFs compare habitat characteristics at ‘used’ and ‘available’ locations to quantify how animals use each habitat type relative to its availability on the landscape. In an SSF, each ‘used’ location (here, an observed location from GPS telemetry) is paired with an arbitrary number of ‘available’ locations, which are simulated based on the distributions of observed step lengths (i.e. movement distances) and turning angles at regular intervals in tracking data. Each observed step is compared with its matched available steps, which accounts for temporal and spatial patterns in habitat availability and autocorrelation in animals’ locations.

First, we sampled each individual’s track to a regular interval, as required by SSFs ([Fortin et al. 2005](#)). We performed analyses at a 60 min interval for all species except canvasbacks, for which we used 3 h data. We included a tolerance of 20% (e.g. 12 min for a 60 min sampling interval, such that steps were between 48 and 72 min apart); any fixes more frequent than this interval were discarded, and any steps outside this interval were not used for calculations. We calculated turning angles and step lengths along each resampled track (‘amt’ package in R; [Signer et al. 2019](#), [www.r-project.org](#)).

We randomly drew from the empirical step length and turning angle distributions to simulate random steps. We used empirical distributions rather than fitting parametric distributions because we had a large sample size and because commonly used parametric distributions (i.e. exponential or gamma for step length; Von Mises for turning angle) fit poorly to our data. This poor fit occurred in part because turning angle distributions were centered around π (180°) rather than 0, which is typical of the back-and-forth ‘commuting’ flights of waterfowl. We drew step lengths and turning angles from the corresponding distribution for each species–season–time of day combination, which means that the definition of available habitat incorporates variation in movement behavior across species, seasons, and diel periods. Seasons were defined following [McDuie et al. \(2019\)](#): pre-hunt/fall (September–October), hunt/winter (November–January), post-hunt/spring (February–April), and summer

(May–August) to capture seasonal behavior (e.g. migration, breeding) and hunting disturbance, which is an important driver of waterfowl movement behavior in this system (Casazza et al. 2012). We also determined time of day (daytime or nighttime) at a step's starting time ('suncalc' package; Thieurmel and Elmarhraoui 2019). We found low correlations between step length and turning angle ($r < 0.3$ between log step length and cosine of turning angle), so we drew step lengths and turning angles independently. We simulated 30 random steps for each observed step.

We extracted data on habitat at the end point of each used or available step at two spatial scales: 300 m and 1 km ('terra' package; Hijmans 2022). We calculated the proportion cover of each habitat type and the mean FLAPS value within 300 m or 1 km circular moving windows, then extracted values of these averaged rasters at the endpoint of the step. Habitat patches in the Central Valley are usually at least 300 m apart (McDuie et al. 2019), so using habitat variables at this scale measures selection at the patch scale; 1 km data represent habitat surrounding a patch and are on the scale of other models of AIV transmission risk between wild birds and poultry (Prosser et al. 2013). For rice, we considered a crop-year to begin on 1 April, which is when rice is planted (Hill et al. 2006), so steps with dates between 1 January and 30 March were linked to the CDL from the prior calendar year.

We then estimated an SSF for each individual–season–time of day–year combination, at each buffer distance. We included only individual–season–time of day–year combinations with at least 50 steps covering at least half the duration of the season, below which we found that it was difficult to reliably estimate model parameters. We used conditional logistic regression in which the response variable was use of each step (a binary variable: used or available) and explanatory variables were: mean FLAPS value at a step's endpoint, proportion herbaceous wetland cover, proportion open water cover, proportion protected land cover, and proportion rice cover. The full model set included all possible combinations of variables, but we only included pairs of variables in a model set if their correlation coefficient within an individual data set was ≤ 0.7 . Models were fit using the *clogit* function ('survival' package; Therneau and Grambsch 2000, Therneau 2022). We then used Akaike information criterion (AICc)-based model averaging to obtain a single SSF for each individual–season–time of day–year–distance combination (Burnham and Anderson 2002); this process was important because differences in habitat composition across the Central Valley (Fleskes et al. 2018) prevented estimation of fully parameterized models in some cases (e.g. because of complete separation). We calculated a conditional average (also called a subset average) of coefficients from all converged models using Akaike weights ('MuMIn' package; Barton 2016). Models not included in this average (e.g. due to lack of convergence or collinearity between variables) were effectively assigned a model weight of zero. Models for each buffer distance (300 m or 1 km) were averaged separately.

Finally, we calculated mean model coefficients from these individual-level average models to estimate habitat selection

for each species, season, time of day, and spatial scale. We only included combinations with at least 10 individuals. These averages were calculated using inverse-variance weighted regression, which calculates the population-level mean selection coefficient as the mean of the individual-level selection coefficients, weighted by the inverse of the standard error (SE) for each coefficient in each individual model (Marzluff et al. 2004, Picardi et al. 2022). When a variable was missing from an individual model but was present as 'available' habitat in that individual's data set, we imputed the coefficient and SE from the model from the same species–season–time of day combination with the lowest (i.e. most negative) coefficient value for that variable (Knopff et al. 2014). This approach allowed us to include these strong avoidance values in our averages; excluding them could have biased our averages towards zero or positive selection.

We evaluated performance of each averaged model by comparing log relative selection strength (log-RSS; Avgar et al. 2017) between observed and random steps. Log-RSS represents the relative selection of a step ending at a given location, compared to a step ending in a location with 'average' available habitat. We used the mean values of land cover variables within the study area (i.e. the Central Valley) as this reference value. For rice, we used 2021 data. We used the Boyce index (Boyce et al. 2002, Hirzel et al. 2006) as our metric of model performance because it is designed for presence-only data ('modEvA' package; Barbosa et al. 2013). This continuous index ranges between -1 and 1 , with higher values indicating better performance and positive values indicating a model that is consistent with the true distribution of presences.

We also calculated variance in coefficient estimates across individuals, time periods, and species to understand which groupings and habitat variables contributed the most to variation in habitat selection. We again used inverse-variance weighted linear regression, then used the SE of the estimated mean as a measurement of the average deviance of a coefficient from the group-level mean selection coefficient. We calculated this variance for each variable for five groupings of the data: 1) individual variation: across all individuals (i.e. data grouped by season, time of day, and year); 2) intraspecific individual variation: across individuals, within species (i.e. data grouped by season, time of day, year, and species); 3) diel variation (i.e. data grouped by individual, season, and year); 4) seasonal variation (i.e. data grouped by individual, time of day, and year); and 5) interannual variation (i.e. data grouped by individual, time of day, and season).

Estimating habitat selection at poultry farms and translating selection to transmission risk

Next, we used our habitat selection results to estimate selection strength at poultry farms in the Central Valley. There is no comprehensive database of farm locations in the USA, so we used data on farm locations from two sources: locations of commercial poultry farms in California (Acosta et al. 2021) and simulated locations of backyard farms (Patyk et al. 2020); simulations are based on a combination of county-level

poultry census data and the FLAPS probability surface. We limited the study area to the Central Valley (defined by Faunt et al. 2009, Faunt 2012), since the Central Valley contains the most intensive poultry farming in California, the highest concentration of our GPS tracking data of wild waterfowl, and was one of the model-training locations for the simulated farm data set (Patyk et al. 2020).

To estimate habitat selection at each farm, we calculated log-RSS for each farm and species–season–time of day combination. We calculated log-RSS using species-level average coefficients, rather than calculating it for each individual model and averaging across individuals (Banner and Higgs 2017) because this allowed us to use inverse-variance weighting for the average log-RSS (above). Because habitat selection results were similar at 300 m and 1 km, we calculated log-RSS at the 300 m scale only.

Disease transmission risk also depends on the abundance of wild birds and on the probability that a bird is actively infected with AIV at the time of contact (among other factors, such as biosecurity measures; Cross et al. 2019). To measure abundance, we used estimates for 2021 from the eBird Status and Trends data set, which provides weekly maps of relative abundance for each species at a 3 km resolution (Fink et al. 2022). We calculated the mean of all weekly estimates in each season (defined as above) to obtain a seasonal abundance map for each species, then averaged abundance values across the study area to obtain a seasonal relative abundance value for each species in our model set. We gathered information on AIV infection prevalence in California waterfowl from published studies (Hill et al. 2012, Bianchini et al. 2021, Teitelbaum et al. 2022), then pooled data across studies

(all of which provided sample sizes as well as infection prevalence) to estimate species-level average winter LPAI prevalence in California. All three studies took place primarily in the winter and all detected LPAI only.

Data supporting analyses are publicly available on the USGS ScienceBase repository (doi: 10.5066/P9I1RS1Z; Teitelbaum et al. 2023b) and code is available at Zenodo (doi: 10.5281/zenodo.10119524; Teitelbaum 2023).

Results

We modeled habitat selection for 446 individuals across 10 waterfowl species and 1552 individual–season–time of day–year combinations (Supporting information).

Most birds avoided poultry habitats within 300 m (i.e. log-RSS < 0), but the strength of avoidance of poultry habitats (measured using the FLAPS probability surface) varied substantially across species, time of day, individuals, and seasons (Fig. 1, Supporting information). The strongest avoidance of poultry habitats was by northern shoveler, cinnamon teal, and mallard (all partial migrants in California). At the 300 m scale, the only species-level averages where selection for poultry habitats was positive were for American wigeon in spring nighttime and canvasback in spring daytime (Fig. 1). For ducks, avoidance of poultry habitats was usually stronger during the day than at night within a given season. There was no consistent seasonal pattern in selection for poultry habitats across species. Patterns of selection were similar at the 1 km scale (Supporting information). All 10 species selected for wetlands in all seasons and diel periods, with stronger selection during daytime (Supporting information).

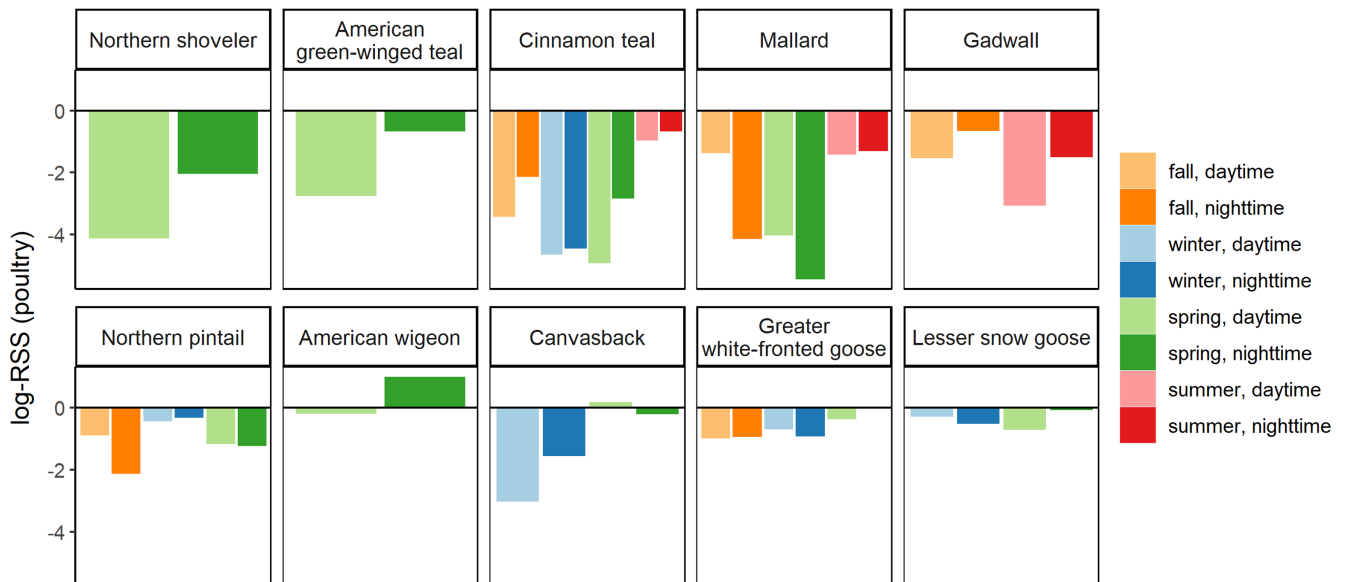


Figure 1. Species-level average selection coefficients for poultry habitats. The y-axis shows log relative selection strength (log-RSS), which can be interpreted as the relative selection for a location that is 100% suitable for poultry farming within 300 m (FLAPS value = 1) compared to one that is entirely unsuitable (FLAPS value = 0), if all other habitat variables in the model remain unchanged. Negative values indicate avoidance of poultry habitats; positive values indicate selection for poultry habitats. Species-level averages are inverse-variance weighted means across all individuals and years. Local and partial migrants are in the top row; long-distance migrants are in the bottom row.

In general, ducks selected for open water, while geese avoided it. Selection for rice and protected areas varied across species, but the strongest selection for rice was in winter and for protected areas was in fall and winter. Model performance was generally high (mean Boyce index = 0.637) but varied across species, seasons, and times of day (Supporting information); average model performance was lowest in fall (0.529) and highest in winter (0.777).

The highest variability in selection for poultry habitats was across diel periods, followed by across years and seasons (Fig. 2). Geese were generally more consistent in their selection than were ducks, across all habitat types (duck selection variance > 10 times higher than goose selection variance for most data groupings and habitats; Fig. 2, Supporting information). Variance in habitat selection was higher for poultry habitats than for wetlands, water, or protected areas (Supporting information). Variation across individuals (both within and among species) was usually lower than variation within individuals; in other words, variation in habitat selection was primarily seasonal, diel, and interannual, rather than inter-individual (Fig. 2).

When we estimated habitat selection at poultry farm locations, we found that most farms were avoided by waterfowl (log-RSS < 0, Fig. 3F). Farms were usually located in areas of high suitability for poultry farming, low protected area cover, low wetland cover, and low open water cover relative to mean values in the study area (Fig. 3A–E). Only 1.5% of commercial farms and 3.5% of backyard farms were within 300 m of a protected area; these farms had the highest average selection strength (Fig. 3D–F), since all species selected for protected areas (Supporting information). Similarly, 13.0% of

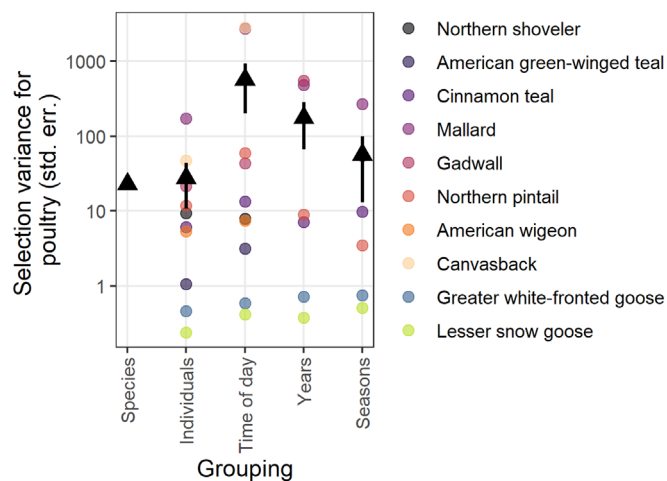


Figure 2. Between- and within-individual variation in selection for poultry habitats at the 300 m scale. Colored dots show means for each species, triangles show grand means across species, and bars show the SE of the mean across species. Variation across species has a single value because it includes all coefficient estimates across all species. Variation across times of day, years, and seasons are calculated within individuals and then averaged (arithmetic mean) for each species. Note the log scale of the y-axis; error bars are asymmetrical because means are arithmetic.

backyard farms and 5.4% of commercial farms were within 300 m of a wetland, which increased selection strength at these farms (Fig. 3A, F), but only 3.4% of the land within 300 m of these farms was wetland. Some farms in the northern Central Valley were near rice farms (16.8% of farms were within 300 m of rice fields, Fig. 3C). Selection strength at these poultry farms was positive in winter because rice was selected primarily in winter, but these farms were avoided in other seasons (Supporting information). Average log-RSS values at farms were slightly lower during night than during the day, but spatial patterns in mean log-RSS were similar across diel periods (Supporting information).

We combined these estimates of habitat selection with information on species' abundances and LPAIV prevalence during winter (Fig. 4). On average, cinnamon teal and canvasback avoided poultry farms more strongly than northern pintail or geese (log-RSS < -0.25; Fig. 4A). Cinnamon teal and canvasback were also the least abundant species in the Central Valley in winter, whereas geese were the most abundant (Fig. 4B). Finally, cinnamon teal and lesser snow goose had the lowest winter LPAIV infection prevalence and northern pintail had the highest (Fig. 4C). Together, these estimates suggest that the risk of waterfowl–poultry AIV transmission in the Central Valley should be lower for cinnamon teal than for northern pintail or geese.

Discussion

Interactions between wildlife and livestock can lead to disease transmission. In the Central Valley of California, waterfowl that carry avian influenza viruses are abundant, as are farming operations with dense poultry populations (Acosta et al. 2021). Here, we analyzed spatiotemporal patterns in selection for poultry habitats by 10 wild waterfowl species in California. We found that waterfowl generally avoided poultry habitats within 300 m and 1 km, and that avoidance varied across species and diel periods; avoidance was generally stronger for short-distance migrants and during the day. When we combined this information with data on poultry farm locations, we found that waterfowl generally avoided poultry farms, but that selection strength was higher at the few farms located near wetlands or protected areas (McDuié et al. 2019). Especially when combined with data on species' abundances and infection prevalence, these results highlight that habitat selection results can inform biosecurity and wildlife management practices by identifying the times and places for which cross-species pathogen transmission is most likely.

Although almost all species avoided poultry farms, avoidance was strongest for cinnamon teal, mallard, and northern shoveler, which reflects differences in species' ecology. Mallard and teal generally select more strongly for dense vegetation compared to other dabbling ducks (Barnum and Euliss 1991, Osborn et al. 2017), and dense vegetation in the Central Valley tends to occur in wetlands (as well as in agricultural drainage ditches). This pattern is particularly notable because

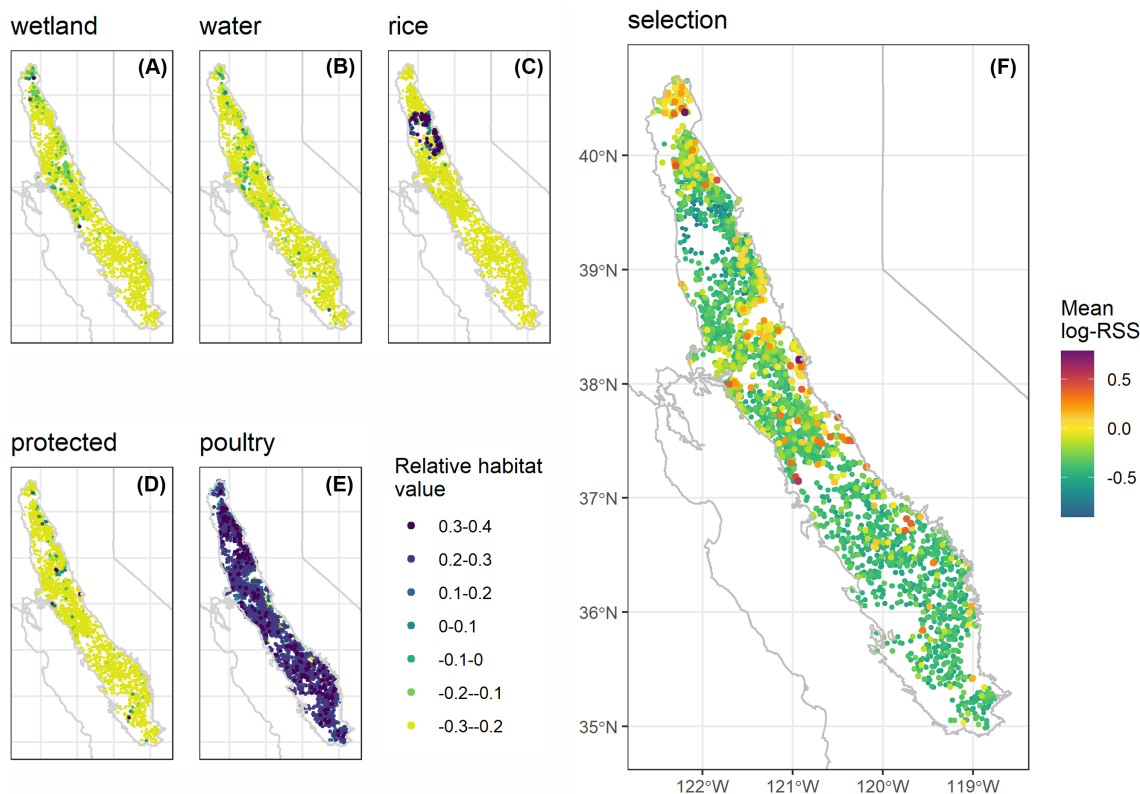


Figure 3. Habitat selection and habitat values at poultry farms in the study area. Each point represents a poultry farm (either a commercial farm or a simulated backyard farm). (A-E) Relative values of each habitat variable at poultry farms. Negative values (light yellow-green) are below the average in the study area, and positive values (dark colors, green to purple) are farms with above-average habitat values. Rice values are based on 2021 data. (F) Mean log relative selection strength (log-RSS) at poultry farms. Values are averaged across species, seasons, and diel periods. Negative values (cool colors: blue and green) indicate avoidance of farms relative to average habitat in the study area. Positive values (warm colors: yellow to red) indicate selection relative to average habitat in the study area. Farms with high positive log-RSS values are plotted slightly larger for visualization. See the Supporting information for maps by farm type, season and time of day.

cinnamon teal are most abundant in the southern Central Valley, where commercial poultry farms are also concentrated, during winter (De Sobrino et al. 2017, Fleskes et al. 2018). Therefore, knowing that cinnamon teal tend to avoid poultry habitats means that the risk of contact with commercial poultry might be smaller than would be expected based on spatial distributions alone. We also saw that long-distance migrants (northern pintail, American wigeon, canvasback, and geese) avoided poultry habitats less strongly than partial or local migrants on average. This higher probability of farm use in migrants is important because pintail and geese are the most abundant species in the Central Valley in winter (Fig. 4, Fleskes et al. 2018, Pandolfino and Handel 2018) and, if infected, they can disperse AIVs to their high-latitude breeding grounds (Gaidet et al. 2010), where cross-continental transmission and reassortment of AIVs is more frequent than at wintering sites (Hill et al. 2017). Understanding species-level differences in habitat selection therefore provides important information about which species are of most concern for AIV transmission and dispersal.

The strongest variation in selection for poultry habitats was across diel periods and seasons, which could inform biosecurity needs at poultry farms. Ducks tend to forage at night

and geese during the day, although all species are behaviorally flexible (Tamisier 1976, Gates et al. 2001, Casazza et al. 2012, Palumbo et al. 2019). The pattern of stronger selection for poultry habitats at night in ducks suggests that continuing to remove food sources from poultry farms remains an important method for discouraging use. In addition, acceptable biosecurity strategies for deterrence depend on the time of day (e.g. loud noises are often unacceptable at night), so deterrence might need to be tailored to time of day that waterfowl tend to be near farms (Atzeni et al. 2016). In contrast, although seasonality in habitat selection was present, it was inconsistent across species, which could pose challenges for identifying seasons when AIV transmission risk is highest. However, because both abundance and AIV infection prevalence vary seasonally (Olsen et al. 2006, Hénaux et al. 2012, Hill et al. 2012, Ely et al. 2013, van Dijk et al. 2014, Samuel et al. 2015), continuing to combine information on species-specific habitat selection and abundance with estimates of infection prevalence across seasons will be important for prioritizing times of heightened biosecurity and AIV surveillance.

Concentrations of suitable wildlife habitat near cities or agricultural areas can attract wildlife into developed areas or,

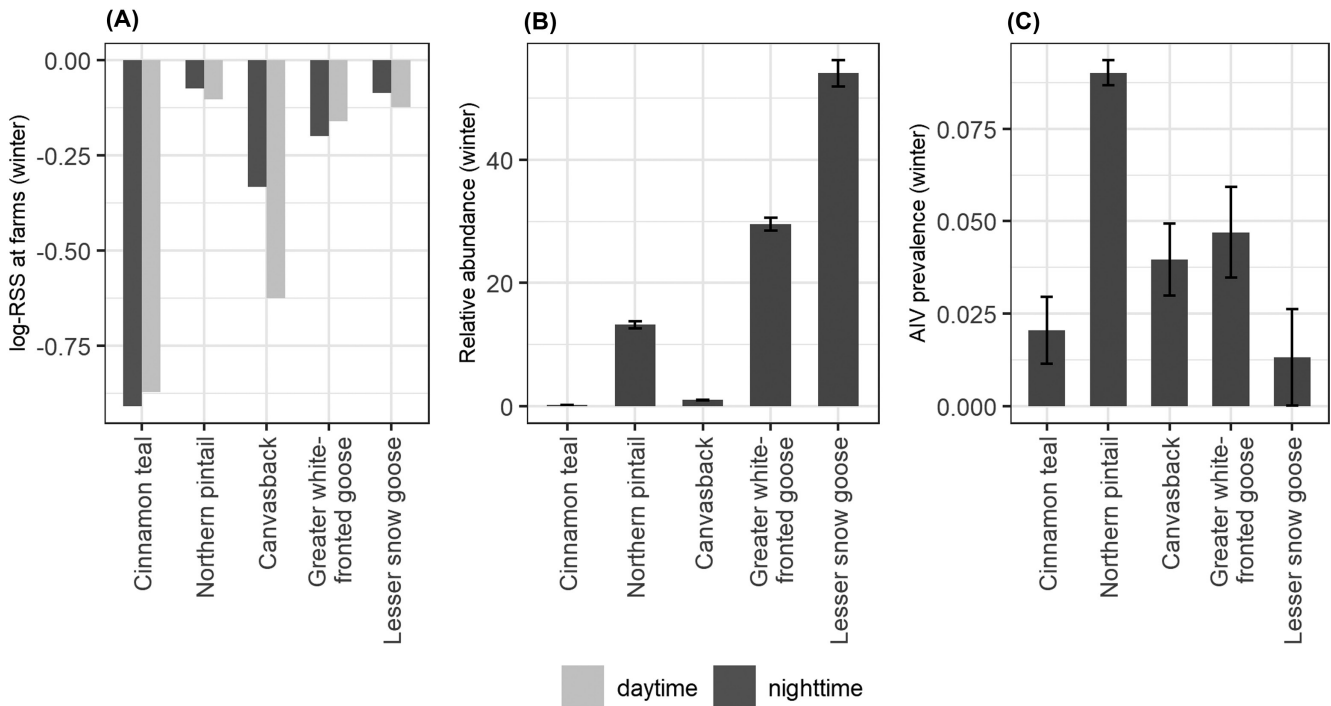


Figure 4. Habitat selection, abundance, and infection prevalence contribute to transmission risk. All plots show estimates for winter in the Central Valley study area. (A) Mean log relative selection strength (log-RSS) at poultry farms. (B) Relative abundance of the same species in the study area. Relative abundance represents numbers of birds. Error bars show SEs of the mean across the study area. (C) Infection prevalence in wintering waterfowl based on field sampling data. Error bars show the SE of the mean. The product of these three components approximates the relative probability of an infected bird from each species using a farm in the Central Valley during winter.

alternatively, can allow wildlife to avoid areas of the highest human development (Wu et al. 2020). Waterfowl move frequently between separate areas for roosting and foraging and suitable habitat patches are rarely contiguous in the Central Valley's highly fragmented landscape (McDuie et al. 2019). Therefore, while having waterfowl habitat near a farm might increase the probability of waterfowl flying nearby or passing through, it might not increase residence times of birds within the boundaries of poultry facilities. Future studies that use genetic information to study the source of AIV outbreaks in poultry and/or wild birds could help clarify when spatial proximity leads to disease transmission. In addition, AIV transmission can occur without direct waterfowl–poultry contact, for example via bridge species, contaminated water, or human movement (Takekawa et al. 2010), so further investigations into the scales of spatial proximity associated with outbreaks could help inform estimates of transmission risk (Velkers et al. 2021). Data on waterfowl abundance could also complement insights from individual-level telemetry by identifying landscape features that are associated with large numbers of birds settling and/or foraging near farms (Acosta et al. 2021). Further, spatial proximity is only one component of disease transmission risk. In the case of AIVs, additional factors that contribute to risk include the current strains circulating (e.g. H5 subtypes, which are the current dominant HPAI viruses); immune status of wild birds to avian influenza viruses; farm size; presence of other wild bird

taxa; and biosecurity precautions that limit direct or indirect contact between wild birds and poultry (Scott et al. 2018, Verhagen et al. 2021, Ayala et al. 2022). Considering the outcome of interest (e.g. economic impact, wild bird health, poultry health) is also important when deciding when and where to prioritize management actions.

California's Central Valley is emblematic of the challenges posed by environmental change for both wildlife and agriculture. Droughts, which are likely to continue to increase in frequency and intensity with anthropogenic climate change (Diffenbaugh et al. 2015), affect the spatial distributions and habitat use of wild birds in the Central Valley (Matchett et al. 2021), and thus potentially their interactions with poultry farms. For example, if drought reduces the quantity or quality of wetland habitat as projected (Matchett and Fleskes 2017), climate change could increase waterfowl use of irrigated agricultural landscapes, including farm ponds. Conversely, limitations on agricultural water use could reduce the attractiveness of agricultural landscapes for waterfowl (Petrie et al. 2016, Matchett et al. 2021). We saw that variation in habitat selection was larger across years than across individuals, presumably linked to inter-annual changes in environmental conditions, which shows that waterfowl can respond quickly to changing habitat availability (Casazza et al. 2021). This pattern mirrors concerns about the effects of environmental change on spillover of other viral infectious diseases (Kessler et al. 2018, Carlson et al. 2022) and could

interact with direct effects of climate change on avian influenza (e.g. environmental persistence; Prosser et al. 2023). Habitat selection models like those we used here could help to predict wildlife distributions and wildlife–poultry contact under future environmental change.

Our results highlight the complex potential connections between wild waterfowl and poultry farms in an area where both waterfowl and poultry farming are abundant. At large spatial scales, data on wildlife abundance could sometimes be sufficient for developing guidelines (e.g. for biosecurity measures or surveillance programs), especially if farms are generally located in unsuitable habitat for wildlife. However, the variation we observed in habitat selection across diel periods, species, and seasons emphasizes that wildlife–poultry interactions depend on individual behavior. Future similar studies would benefit from more precise and reliable information on farm locations and land cover. For example, some of the poultry data we used were simulated, which prohibits identifying individual farms at high risk of contact with wildlife. Similarly, our land cover data were static or at an annual temporal resolution; using daily or monthly information could more accurately predict habitat selection, for example by incorporating wetland depth or rice harvest (Matchett et al. 2021). These patterns could also differ in other regions or systems, for example where free-range livestock are common (Barasona et al. 2014, Prosser et al. 2016b), so integrating data on livestock behavior and management is another important variable for predicting transmission risk. Together, these data can identify places and times of the highest risk of wildlife–livestock contact, which supports effective disease prevention and management strategies.

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Data availability statement

Data necessary to reproduce step-selection analyses are archived at USGS ScienceBase (doi: [10.5066/P9I1RS1Z](https://doi.org/10.5066/P9I1RS1Z), Teitelbaum et al. 2023b) and code to reproduce all analyses is available at Zenodo (<https://doi.org/10.5281/zenodo.10119523>, Teitelbaum et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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