RESEARCH ARTICLE



Protection of wetlands as a strategy for reducing the spread of avian influenza from migratory waterfowl

Tong Wu, Charles Perrings, Chenwei Shang, James P. Collins, Peter Daszak, Ann Kinzig, Ben A. Minteer

Received: 23 April 2019/Revised: 29 July 2019/Accepted: 1 August 2019/Published online: 22 August 2019

Abstract Highly pathogenic avian influenza (HPAI) H5N1 has led to the death or destruction of millions of domesticated and wild birds and caused hundreds of human deaths worldwide. As with other HPAIs, H5N1 outbreaks among poultry have generally been caused by contact with infected migratory waterfowl at the interface of wildlands and human-dominated landscapes. Using a case-control epidemiological approach, we analyzed the relation between habitat protection and H5N1 outbreaks in China from 2004 to 2017. We found that while proximity to unprotected waterfowl habitats and rice paddy generally increased outbreak risk, proximity to the most highly protected habitats (e.g., Ramsar-designated lakes and wetlands) had the opposite effect. Protection likely involves two mechanisms: the separation of wild waterfowl and poultry populations and the diversion of wild waterfowl from human-dominated landscapes toward protected natural habitats. Wetland protection could therefore be an effective means to control avian influenza while also contributing to avian conservation.

Keywords Avian conservation · Avian influenza · China · Protected areas · Ramsar · Wetlands

INTRODUCTION

Although habitat protection is recognized to be essential for wild species preservation, protected area design has been changing to embrace broader social and environmental considerations (Xu et al. 2017; Barnes et al. 2018).

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13280-019-01238-2) contains supplementary material, which is available to authorized users.

There now exist a wide range of nominally protected areas that vary in size, proximity to human activities, and the environmental benefits to be protected. In addition to larger remote habitats aimed primarily at wild species preservation, there are many smaller protected areas located in human-dominated landscapes, such as farmlands, that are aimed at maintaining particular ecosystem services (Fischer et al. 2008; Railsback and Johnson 2014). The degree of protection offered to habitats also varies across protected areas. Humans and their domesticates may have very limited access to wild habitat in highly protected areas, but face few restrictions in "paper parks" or protected areas focused on other environmental benefits (Di Minin and Toivonen 2015). In such cases interactions between wild and domesticated species at park boundaries may have negative effects, including cross-species disease transmission (Daszak et al. 2000).

Most emerging zoonotic and epizootic diseases originate at the interface between managed landscapes and wildlands (Jones et al. 2008; Gruber 2017). Since wildlands are frequently subject to some form of protection, the role of protected areas in pathogen transmission between domesticated species or humans and wildlife is an important topic for research (Kilpatrick et al. 2017). In this paper we consider how outbreaks of highly pathogenic avian influenza (HPAI) H5N1, one of the most widespread and fatal (to both domesticates and humans) zoonoses of recent decades, are related to the degree of protection given to waterfowl habitats in the country of origin of most HPAIs, China.

Migrating waterfowl are known to spread avian influenza, and China is particularly vulnerable because it is traversed by three globally important migratory bird flyways (Fig. 1). These flyways connect large numbers of natural and human-made waterfowl habitats (Fig. 2) in



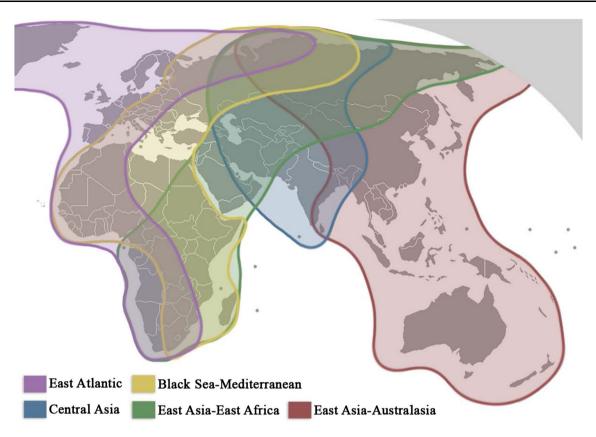


Fig. 1 The major migratory bird flyways that cover Africa, Europe, and Asia. The ones that cover China are the East Asia-Australasia, Central Asia, and East Africa-Asia flyways

which the likelihood of wild and domesticated birds coming into contact varies widely. In unprotected lakes, wetlands, and paddy fields, for example, wild waterfowl frequently come into contact with free-ranging chickens, ducks, and geese in conditions of weak biosecurity (Conan et al. 2012; USDA Foreign Agricultural Service 2017). In more highly protected wildfowl habitats, on the other hand, restrictions on access may limit contact between wild and domesticated birds (Higuchi et al. 2004; Liu et al. 2005; Olsen et al. 2006; Tian et al. 2015).

Consider the case of Poyang Lake, China's largest freshwater lake and home to approximately fifty million free-ranging poultry and up to one million wintering wild birds (Xiao et al. 2010). While the Poyang Lake area has been identified as a potential avian influenza hotspot (Prosser et al. 2013), the incidence of H5N1 poultry outbreaks in the neighborhood of the lake is much lower than would be expected from the convergence of risk factors (Takekawa et al. 2010). What differentiates Poyang Lake from other such areas is that measures are in place to limit direct contact between wild and domesticated birds. Poyang Lake has been designated as a Ramsar Convention "Wetland of International Importance especially as Waterfowl Habitat." The Ramsar Convention, an international agreement created in 1971 with 170 national

signatories, aims to promote the "wise use" of wetlands by requiring signatories to limit activities such as rice cultivation and livestock husbandry through zoning and other policies (Ramsar Convention Secretariat 2010b).

The convention does not mandate universal restrictions but provides guidance on the types of human activities considered permissible given local ecological conditions and objectives, including migratory waterfowl conservation. In terms of its specific guidelines for managing avian influenza risks, the Ramsar Convention's official handbook recommends managers to "physically separate wild birds and domestic/captive birds (including poultry), their food and water sources, and their waste where this is feasible" (Ramsar Convention Secretariat 2010a). In China, authorities have enforced tight restrictions on agriculture and husbandry around Poyang Lake and other Ramsar sites to preserve migratory bird habitats (Finlayson et al. 2010; Han et al. 2015). More generally, Ramsar sites have been effective in reducing anthropogenic pressures on natural habitats and promoting waterfowl abundance (Kleijin et al. 2014; Zhang et al. 2019).

In this paper, we consider the impact of Ramsar status on the probability of transmission of avian influenza between wild and domesticated bird populations. More particularly, we consider whether the degree of protection



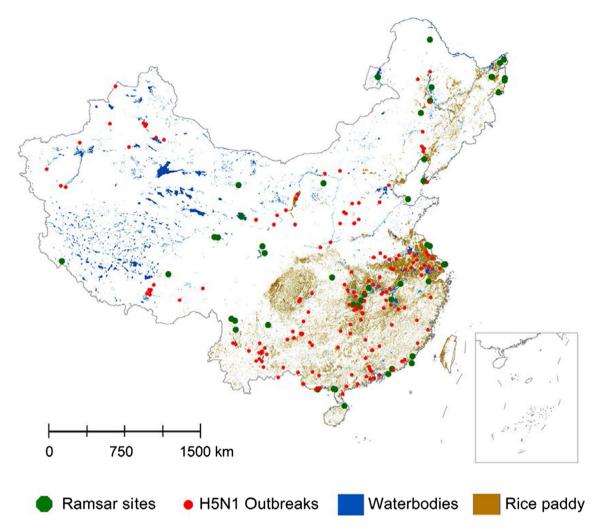


Fig. 2 The distribution of HPAI H5N1 poultry outbreaks relative to waterbodies, Ramsar sites and rice paddies in China

of waterfowl habitats affects the probability of H5N1 outbreaks in proximate poultry populations. To do this we used a case-control approach to analyze the location of H5N1 poultry outbreaks between January 1, 2004 and September 1, 2017 relative to habitats characterized by different rates of wild bird-poultry contact, while controlling for general biosecurity levels. While there are no reliable time-series data on the distribution of wildfowl and free-ranging poultry in China, there are data on habitats and habitat protection—extending from rice paddy cover, which is a common habitat for domesticated fowl, to fully protected wildfowl habitats. Exposure is measured by the proximity of poultry populations to habitats attractive to wildfowl, and the measures taken to restrict contact between poultry and wildfowl in those habitats. We expected outbreaks in poultry populations in close proximity to habitats attractive to wildfowl to be more frequent when those habitats were unprotected or weakly protected, and less frequent when they were strongly protected.

MATERIALS AND METHODS

Data sources

Our data span the period January 2004 to September 2017, during which time there were 201 reported HPAI H5N1 poultry outbreaks. Data on H5N1 outbreaks in China include the location and dates of outbreaks, and derive from the Emergency Prevention System for Animal Health (EMPRES), a joint project of the United Nations' Food and Agriculture Organization and the World Organization for Animal Health (Welte and Teran 2004). Data on waterfowl habitat, including rice paddies, open waterbodies, and wetlands, derive from the Institute of Geography at the



Chinese Academy of Sciences and the Center for Human–Environment Systems Sustainability at Beijing Normal University. We combined baseline maps from Landsat TM imagery with data on elevation, temperature, and precipitation, along with 6 major and 25 subsidiary land cover classification types (Table S1), following the methodology reported in Zhang et al. (2014). Data on Ramsar sites derive from the official database of the Ramsar Convention (http://www.ramsar.org/). During the study period, there were 48 Ramsar sites, all associated with large waterbodies and their wetlands.

We did not have direct data on biosecurity measures at different locations, but exploited the fact that a number of studies have revealed a strong positive correlation between biosecurity and measures of economic development such as per-capita Gross Domestic Product (GDP) (Hennessy and Wang 2012). Data on per-capita GDP derive from the databases and statistical yearbooks published by the National Bureau of Statistics of China (National Bureau of Statistics 2016). These data vary in availability and quality across prefectures (a sub-provincial administrative unit). Where there were gaps in prefectural economic data, missing values were interpolated as a linear time series trend from data for previous and later years or substituted by contemporary provincial-level values. 17 out of 1206 values for per-capita GDP in the reported model were interpolated this way.

Case-control approach

We used a case-control approach, in which the spatial locations of H5N1 poultry outbreaks with respect to habitats attractive to wildfowl were treated as the population of cases, and randomly selected uninfected locations were treated as the population of controls (at a ratio of 5 controls per case). The case–control approach allows a comparative population-level analysis of disease risk factors. It generates odds ratios that are a measure of relative risk and that are particularly helpful when used to assess diseases with a low incidence rate—what is known as the "rare disease assumption" (Greenland and Thomas 1982; Schulz and Grimes 2002). While the approach has some limitations, particularly with respect to selection bias, its relatively flexible data requirements and efficiency of use has encouraged its widespread application in epidemiology (Breslow 1996; Grimes and Schulz 2005). Applications range from non-communicative pathologies, such as mental health disorders and cancer, to a wide range of infectious diseases (Yusuf et al. 2004; Jha et al. 2008; O'Donnell et al. 2016), including HIV-AIDS (Schulz and Grimes 2002).

Avian influenza, whether in terms of poultry or human cases, has a low incidence rate, and thus meets the "rare

disease assumption". We implemented the approach through the random selection of locations over the study area—mainland China—using the random coordinates generator algorithm in ArcGIS. The spatial limits for the random distribution of points were initially specified as the national boundary, but we later specified sub-national boundaries in alternative models. The controls were randomly generated so as to avoid bias to the locations of waterfowl habitats compared with the distribution of cases. Other studies of environmental risk factors in avian influenza have used this same technique to identify cases by outbreak coordinates or administrative units, and controls by random selection of uninfected locations (the randomness producing a representative sample).

One challenge of this approach is the potential presence of confounders: variables that influence both the independent exposure variable and the dependent disease variable, leading to a spurious relation between the two. In our case, a confounder would be one that separately influences both the probability of an outbreak in a given location and the degree to which proximate wildfowl habitat is protected. In traditional cohort-based epidemiological studies the effect is managed through restriction of controls to those that are not correlated with an identified confounder, matching the distribution of controls to that of cases, and random allocation of controls to exposure so the distribution of both known and unknown confounders is similar for the groups being compared (Kirkwood and Sterne 2003). In this study, we tried to minimize the effects of potential confounders by random allocation of controls to exposure (detailed below), and by using multiple methods of random allocation. This follows the approach taken by Fang et al. (2008) and Fang et al. (2013) in their respective analyses of the environmental drivers of H5N1 and H7N9 in China (both studies also used a ratio of 5 controls for every 1 case).

Spatial analysis

The land cover raster dataset and the Ramsar wetland dataset were inputted into the GIS software package Arc-Map 10.4 to calculate the values of the explanatory variables. The resolution of the dataset was 1000 m, and the map reference year was 2010. Accurate land cover maps were not available annually, and the 2010 land cover distribution was used as the best available spatial "average". We note, however, that land cover for wetland and rice paddy at this resolution did not change significantly over our study period. Each outbreak (case) was placed on the land cover map based on reported coordinates of the location in which it was first observed. The locations of the controls were generated using the random points generator algorithm in ArcMap, and distributed across the map of China (Model 1; Table S2). Two alternative sets of controls



were also randomly generated. The first comprised 5 controls for each prefecture, regardless of the size of the prefecture. This set accounts for the geographically uneven distribution of populations (Model 2; Table S3). The second comprised 5 controls for each case within a given province (Model 3; Table S4). Controls were randomly distributed within the boundaries of each prefecture or province. (There were five mainland provinces without reported cases during the study period: Hainan, Sichuan, Heilongjiang, Beijing, and Shandong.)

Proximity to the edge of the nearest Ramsar site was calculated along a normalized scale of 100, proportional to the most distant case/control location: proximity = ((maximum distance - location distance)/maximum-distance)*100. A proximity value of 100 represents maximal proximity, e.g., the location of the outbreak is within the Ramsar site, while a proximity value of 0 represents maximal distance away from the site within the range of values. The Ramsar site identified also had to be contemporary to the outbreak (i.e., the site had to have acceded to the convention at least one year before the outbreak). Proximity to the nearest unprotected large waterbody—i.e., waterbodies larger than 1 sq. km—was also calculated along a normalized scale of 100. For the rice paddy variable, each outbreak was given a 10-km radius buffer zone (alternatives of 20-km and 50-km were also tested), and the area in that buffer zone covered by rice paddy was estimated. The per-capita GDP value associated with each case/control was the officially reported value for the prefecture in which the outbreak was observed, or that in which the control was randomly placed, for the year of occurrence.

Statistical analysis

The data generated by the GIS analysis were used to estimate a set of multivariate logistic regression models. The general form of the models was:

$$Pr(y_i = 1) = \exp(\theta_i) / (\exp(\theta_i) + 1),$$

$$\theta_i = \alpha_0 + \sum_i^4 X_{ij} \beta_i + \varepsilon_i,$$

where $\Pr(y_i = 1)$ is the likelihood of a H5N1 poultry outbreak at location i ($y_i = 0$ in the absence of an outbreak), α_0 is the intercept, ε is the error term, and X_i is the risk factors at location i. These risk factors include: the proximity of the location to the nearest Ramsar site; the proximity of the location to the nearest large waterbody; the amount of rice paddy land cover within a 10-km (or 20-km or 50-km) radius buffer zone around the location; and the per-capita GDP of the prefecture in which the case/control was located (a proxy for the effectiveness of biosecurity and environmental protection). General linear models of this

kind have frequently been used in epidemiological studies of avian influenza, including for H5N1 in wild birds and poultry (Fang et al. 2008; Si et al. 2010; Fang et al. 2013; Si et al. 2013). This study extended the analysis by focusing explicitly on the epidemiological effect of protected areas, which the existing literature has ignored.

RESULTS

Across all models, the risk factors analyzed in our study were found to be below the 0.1% *p* value threshold (Table 1; Fig. 3). Proximity to a Ramsar site was found to reduce the risk of an H5N1 poultry outbreak, whereas proximity to a large unprotected waterbody and the density of rice paddies within a buffer area were both found to increase outbreak risk (Fig. 4). We also found that our indirect proxy for biosecurity, the per-capita GDP of an area, was negatively related to the likelihood of an outbreak.

We found that a unit increase in proximity (~ 17.6 km) to the nearest Ramsar site (i.e., along a scale of 0–100, with 0 being the farthest distance recorded in the dataset; see Methods) was associated with a 3.2% reduction in the odds of an H5N1outbreak. By contrast, a unit increase in proximity (~ 1.5 km) to the nearest unprotected waterbody was associated with a 7.7% increase in the odds of an H5N1outbreak. Within a 10-km radius buffer zone, an increase of 1% in rice paddy land cover was associated with up to a 1.6% increase in the odds of an outbreak. And in a given prefecture, a 1000 RMB (~ 147 US\$ in 2018) increase in per-capita GDP was associated with a 2% decline in the odds of an outbreak.

The average number of cases per outbreak was 3045. The average number of poultry lost due to infection was 2620 per outbreak, while that due to culling was a much larger 96,227 per outbreak. Using these parameters, and all else being equal, a unit (17-km) increase in proximity to a highly protected waterfowl habitat reduced expected poultry mortality (total deaths from infection and culling) by approximately 3160 birds. A unit (~ 1.5-km) increase in proximity to an unprotected habitat increased expected poultry mortality by 7610 birds. As of 2019, the average price of a frozen, supermarket chicken in Beijing was approximately 40 RMB (~ 5.88 US\$ in 2018), while that for live, free-range chickens and for ducks, geese, and other types of poultry (both frozen and live) were several times higher (http://www.xinfadi.com.cn/). Using the lower-end price of 40 RMB per bird, a conservative estimate for the value of disease mitigation from being 17 km closer to a Ramsar wetland was approximately 126,400 RMB $(\sim 18,865 \text{ US} \$ \text{ in } 2019).$



Table 1 Results for models of risk factors of H5N1 poultry outbreaks in China, from January 1, 2004 to September 20, 2017. Odds ratios and *p*-levels are reported (latter in parentheses). All are significant at the 1-percent level. Results from columns (a), (b), and (c) differed because of different values for rice paddy area radius

Variables	Units	(a)	(b)	(c)
Model 1				
Proximity to nearest unprotected large water body	_	1.0051 (0.000)	1.0455 (0.000)	1.0418 (0.000)
Proximity to nearest Ramsar wetland	_	0.98326 (0.001)	0.97906 (0.000)	0.97633 (0.000)
Rice paddy area				
Within 10-km radius zone	km^2	1.0163 (0.000)		
Within 20-km radius zone	km^2		1.0052 (0.000)	
Within 50-km radius zone	km^2			1.0010 (0.000)
Per-capita GDP	¥	0.99999 (0.000)	0.99999 (0.000)	0.99998 (0.000)
Observations		1206	1206	1206
Pseudo R ²		0.1940	0.2205	0.2293
Model 2				
Proximity to nearest unprotected large water body	_	1.0777 (0.000)	1.0735 (0.000)	1.0715 (0.000)
Proximity to nearest Ramsar wetland	_	0.97168 (0.000)	0.96936 (0.000)	0.96834 (0.000)
Rice paddy area				
Within 10-km radius zone	km^2	1.0065 (0.000)		
Within 20-km radius zone	km^2		1.0022 (0.000)	
Within 50-km radius zone	km^2			1.0004 (0.000)
Per-capita GDP	¥	0.99998 (0.000)	0.99998 (0.000)	0.99998 (0.000)
Observations		1356	1356	1356
Pseudo R ²		0.1476	0.1571	0.1571
Model 3				
Proximity to nearest unprotected large water body	_	1.0563 (0.000)	1.0546 (0.000)	1.0551 (0.000)
Proximity to nearest Ramsar wetland	_	0.98474 (0.002)	0.98333 (0.001)	0.98370 (0.002)
Rice paddy area				
Within 10-km radius zone	km^2	1.0041 (0.003)		
Within 20-km radius zone	km^2		1.0013 (0.001)	
Within 50-km radius zone	km^2			1.0002 (0.004)
Per-capita GDP	¥	0.99999 (0.000)	0.99999 (0.000)	0.99999 (0.000)
Observations		1206	1206	1206
Pseudo R ²		0.0861	0.0883	0.0856

The variables "Proximity to nearest unprotected large water body" and "Proximity to nearest Ramsar wetland" were unit-less because they were normalized

DISCUSSION

Avian influenza risk mitigation has so far relied heavily on poultry vaccination and the monitoring and management of poultry supply chains. However, implementation of these measures at sufficiently large scales and for long enough to contain disease risks is costly and logistically challenging, and transmission can occur even among vaccinated flocks (Poetri et al. 2014). Furthermore, while vaccination may offer protection against circulating strains, it provides no guarantee against other emerging influenza viruses. Policies that lower the probability of disease transmission through the segregation of wild and domesticated birds in and around protected areas may be a cost-effective

supplement to the vaccination of high-risk flocks, and to postoutbreak suppression measures.

Our findings suggest that strict protection (e.g., Ramsar-like restrictions on agriculture, husbandry, and other intensive human activities) of wetlands and lakes—the most important migratory waterfowl habitat—may be an effective way to reduce avian influenza risks. We conjecture that this involves two mechanisms: the exclusion of domesticated birds from wildfowl habitat and the diversion of wildfowl from heavily impacted, unprotected habitat such as paddy fields toward protected areas. First, restrictions on agriculture and husbandry within and around protected areas likely reduce contact between infected wild waterfowl and susceptible poultry. We used Ramsar status



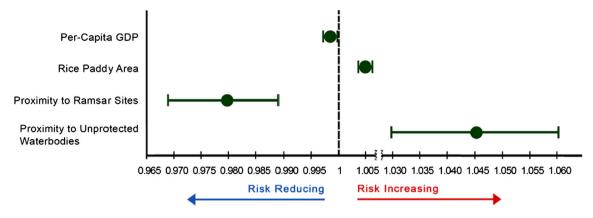


Fig. 3 The relative risks of environmental and socioeconomic predictors in HPAI H5N1 poultry outbreaks (Model 1). Odds ratios and 95% confidence intervals are shown for each risk factor

as a proxy for the existence of effective buffer zones, since a central feature of Ramsar sites in China is the prohibition of such activities in and around the protected area (Wang et al. 2012; Jiang et al. 2015). Second, the diversion of migratory waterfowl away from farmlands—particularly paddy fields-likely reduces the abundance of infected waterfowl in human-dominated, and therefore poultryabundant, areas. For instance, according to decadal surveys of the Poyang Lake area, waterfowl numbers and diversity have been increasing in protected wetland habitats relative to surrounding farmlands and unprotected waterbodies (Wu et al. 2014). This is consistent with the widely observed preference of migratory birds for natural lakes and wetlands over farmlands and other human-dominated landscapes (Bonter et al. 2009; Li et al. 2013; Beatty et al. 2014).

A limitation of the study is that there are no reliable census data on wild and domesticated bird abundance in these different habitats. Indeed, this is a general problem in migratory waterfowl conservation, particularly with respect to multi-species congregations (Haig et al. 1998). There is, however, indirect evidence that waterfowl abundance in both environments is "high". And in China, it has been found that wetland size is a good predictor of wild waterfowl population size and density (Zhang et al. 2015). Among the criteria for designation as a Ramsar site, a given location should regularly support at least 20 000 waterbirds (Criterion 5) and/or 1% of the population of a waterbird species or sub-species (Criterion 6) (Ramsar Convention Secretariat 2019). Among the 48 mainland China Ramsar sites in our study period, 32 met Criterion 5 and 29 met Criterion 6. Rice paddies have also been strongly associated with free-ranging poultry in China and other parts of Asia (Muzaffar et al. 2010). Since migratory waterfowl prefers natural lakes and wetlands to humandominated sites, farmlands in China benefit from the same diversion effect that has been observed for wild birds displaced to natural refugia in other parts of the world (Gill et al. 2001; Beatty et al. 2014).

Since per-capita GDP has been shown to be a proxy for the general quality of public health infrastructure, environmental protection, and biosecurity in livestock production and distribution (Hennessy and Wang 2012), we expected biosecurity in both poultry production and waterfowl habitat protection to be increasing in per-capita GDP. We found a similar "modernization effect" in previous provincial-level analyses of H5N1 outbreaks in China (Wu and Perrings 2017). At the same time, since higher income also stimulates the production and consumption of meat, it is likely to have some risk-increasing effects. Our results showed that on balance, more affluent areas in China experienced lower risk. This is also consistent with global evidence that more affluent, bettergoverned countries are more effective at enforcing protected areas and implementing waterfowl conservation (Amano et al. 2018). However, the small effect size indicates that only large differences in income have significant real-world effects in terms of epidemic mitigation—likely a reflection of the high costs associated with effective biosecurity and habitat protection enforcement.

CONCLUSION

China is in the process of establishing a national park system to standardize and enhance wildlife habitat protection across the country. While current protected areas have been relatively successful at avian conservation, there is still scope for the expansion and consolidation of the country's protected areas to better protect waterfowl habitat and therefore mitigate infectious disease risk (Xu et al. 2017; Zhang et al. 2017). In the longer term, there is also the need to mitigate the risks from climate change. Over the coming decades, projected changes in temperature

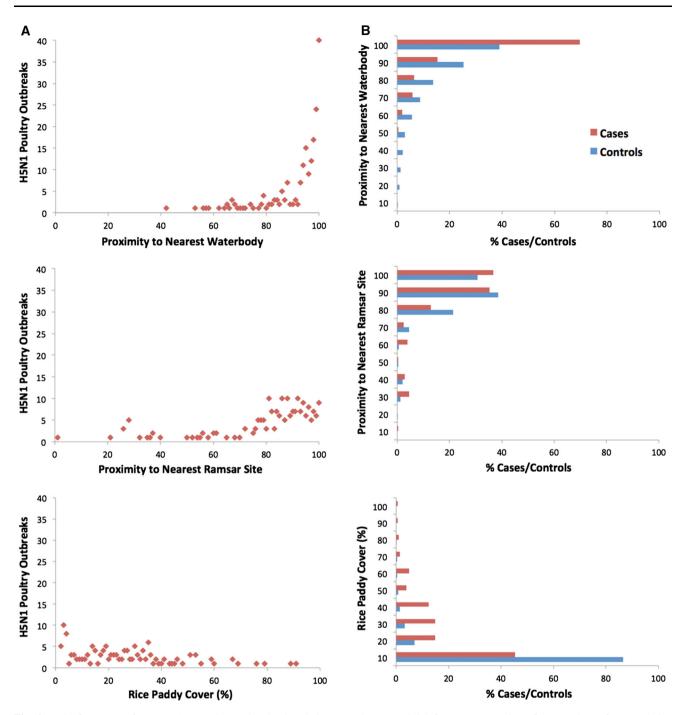


Fig. 4 a The frequency of cases (H5N1 poultry outbreaks) in relation to environmental risk factors (scatter plots). **b** Proportions of cases relative to controls (bar charts). For proximity to waterbodies and rice paddy cover, the proportions of cases relative to controls showed the former to be more frequent than would be expected by chance alone. For proximity to Ramsar sites, the proportions showed cases to be less frequent than would be expected by chance alone. *Note* Proximity to waterbodies and Ramsar sites was measured as a normalized index of 100, with 100 being most proximate and 0 being least; rice paddy cover was measured as the percent of land within a 20-km radius buffer zone (10-km and 50-km buffer zones were also analyzed; please see SI Table S1)

and precipitation, along with their impacts on habitat suitability and bird migration patterns, could significantly alter the ecology and evolution of avian influenza in East Asia (Morin et al. 2018). In the Poyang Lake area for instance, climate change is expected to interact with

agricultural and other land use changes to alter landscape structure, with significant implications for the population dynamics of livestock and wildlife (Yan et al. 2013). Therefore, in the management of Ramsar sites and other protected areas, China should adopt a dynamic approach to



governance that anticipates and mitigates such risks—which, with respect to large-scale epidemics, is likely to be economically efficient in the long run (Pike et al. 2014).

In this study, we have focused on Ramsar sites largely because of their importance as waterfowl habitat and their mandated exclusion of compromising economic activities, but the important elements in the mitigation of disease risk do not depend on Ramsar status. The epidemiological effect found in our study may be a globally generalizable strategy, at least for avian influenza. Previous studies have suggested that widespread public concern about the role of wild birds in the spread of avian influenza could undermine peoples' willingness to pay for migratory bird conservation (Brouwer et al. 2008). Providing scientific evidence for avian conservation as a form of public health investment could therefore help conservation efforts overcome this problem.

It is worth noting that the results of this study reinforce arguments for separating domesticated species and wildlife habitats as a way of limiting anthropogenic impacts on ecosystems and the biodiversity they support (Wilson 2016). While our concern has been the transmission of H5N1 from infected wild birds to susceptible poultry, the risk goes both ways, as cross-species contact creates disease risks for wildlife populations as well. Indeed, since disease is now implicated in the extinction of at least some wild species, limiting cross-species contact may offer further, important conservation benefits.

Finally, migratory bird habitats are relatively poorly protected across the world. Given China's large landmass and central position along migratory bird corridors (Yong et al. 2018), the protection of natural habitats in China could have a disproportionate impact on wild waterfowl conservation overall. Ensuring the ecological integrity of the lakes and wetlands used by migratory waterfowl not only safeguards poultry, and therefore human health, but also advances the long-term prospects of the wild birds themselves.

Acknowledgments Funding was provided by NSF-NIH-USDA Ecology and Evolution of Infectious Diseases Program (Grant Number 1414374).

REFERENCES

- Amano, T., T. Székely, B. Sandel, S. Nagy, T. Mundkur, T. Langendoen, D. Blanco, C.U. Soykan, et al. 2018. Successful conservation of global waterbird populations depends on effective governance. *Nature* 553: 199.
- Barnes, M.D., L. Glew, C. Wyborn, and I.D. Craigie. 2018. Prevent perverse outcomes from global protected area policy. *Nature Ecology & Evolution* 2: 759–762.

- Beatty, W.S., D.C. Kesler, E.B. Webb, A.H. Raedeke, L.W. Naylor, and D.D. Humburg. 2014. The role of protected area wetlands in waterfowl habitat conservation: Implications for protected area network design. *Biological Conservation* 176: 144–152.
- Bonter, D.N., S.A. Gauthreaux Jr., and T.M. Donovan. 2009. Characteristics of important stopover locations for migrating birds: Remote sensing with radar in the Great Lakes basin. *Conservation Biology* 23: 440–448.
- Breslow, N.E. 1996. Statistics in epidemiology: The case-control study. *Journal of the American Statistical Association* 91: 14–28.
- Brouwer, R., P. van Beukering, and E. Sultanian. 2008. The impact of the bird flu on public willingness to pay for the protection of migratory birds. *Ecological Economics* 64: 575–585.
- Conan, A., F.L. Goutard, S. Sorn, and S. Vong. 2012. Biosecurity measures for backyard poultry in developing countries: A systematic review. BMC Veterinary Research 8: 240.
- Daszak, P., A.A. Cunningham, and A.D. Hyatt. 2000. Wildlife ecology—Emerging infectious diseases of wildlife—Threats to biodiversity and human health. *Science* 287: 443–449.
- Di Minin, E., and T. Toivonen. 2015. Global protected area expansion: Creating more than paper parks. *BioScience* 65: 637–638.
- Fang, L.-Q., S.J. de Vlas, S. Liang, C.W.N. Looman, P. Gong, B. Xu, L. Yan, H. Yang, et al. 2008. Environmental factors contributing to the spread of H5N1 Avian influenza in mainland China. *PLoS ONE* 3: e2268.
- Fang, L.Q., X.L. Li, K. Liu, Y.J. Li, H.W. Yao, S. Liang, Y. Yang, Z.J. Feng, et al. 2013. Mapping spread and risk of avian influenza A (H7N9) in China. Scientific Reports 3: 2722.
- Finlayson, M., J. Harris, M. McCartney, Y. Lew, and C. Zhang. 2010. Report on Ramsar visit to Poyang Lake Ramsar site, P. R. China. Secretariat of the Ramsar Convention.
- Fischer, J., B. Brosi, G.C. Daily, P.R. Ehrlich, G. Rebecca, J. Goldstein, D.B. Lindenmayer, A.D. Manning, et al. 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment 6: 380–385.
- Gill, J.A., K. Norris, P.M. Potts, T.G. Gunnarsson, P.W. Atkinson, and W.J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. *Nature* 412: 436–438.
- Greenland, S., and D.C. Thomas. 1982. On the need for the rare disease assumption in case-control studies. *American Journal of Epidemiology* 116: 547–553.
- Grimes, D.A., and K.F. Schulz. 2005. Compared to what? Finding controls for case-control studies. *The Lancet* 365: 1429–1433.
- Gruber, K. 2017. Predicting zoonoses. Nature Ecology & Evolution 1: 1-4.
- Haig, S.M., D.W. Mehlman, and L.W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12: 749–758.
- Han, X., X. Chen, and L. Feng. 2015. Four decades of winter wetland changes in Poyang Lake based on Landsat observations between 1973 and 2013. Remote Sensing of Environment 156: 426–437.
- Hennessy, D.A., and T. Wang. 2012. Animal disease and the industrialization of agriculture. In *Health and animal agriculture* in developing countries, ed. D. Zilberman, J. Otte, D. Roland-Holst, and D. Pfeiffer. Heidelberg: Health and Animal Agriculture in Developing Countries. Food and Agriculture Organization of the United Nations and Springer Science & Business Media.
- Higuchi, H., J.P. Pierre, V. Krever, V. Andronov, G. Fujita, K. Ozaki, O. Goroshko, M. Ueta, et al. 2004. Using a remote technology in conservation: Satellite tracking white-naped cranes in Russia and Asia. *Conservation Biology* 18: 136–147.
- Jha, P., B. Jacob, V. Gajalakshmi, P.C. Gupta, N. Dhingra, R. Kumar, D.N. Sinha, R.P. Dikshit, et al. 2008. A nationally representative



case–control study of smoking and death in India. *New England Journal of Medicine* 358: 1137–1147.

- Jiang, B., C.P. Wong, Y. Chen, L. Cui, and Z. Ouyang. 2015. Advancing wetland policies using ecosystem services-China's way out. Wetlands 35: 983-995.
- Jones, K.E., N.G. Patel, M.A. Levy, A. Storeygard, D. Balk, J.L. Gittleman, and P. Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451: 990–994.
- Kilpatrick, A.M., D.J. Salkeld, G. Titcomb, and M.B. Hahn. 2017. Conservation of biodiversity as a strategy for improving human health and well-being. *Philosophical Transactions of the Royal* Society B: Biological Sciences 372: 20160131.
- Kirkwood, B., and J. Sterne. 2003. Essential Medical Statistics, 2nd ed. London: Wiley-Blackwell.
- Kleijin, D., I. Cherkaoui, P.W. Goedhart, J. Hout, and D. Lammertsma. 2014. Waterbirds increase more rapidly in Ramsar-designated wetlands than in unprotected wetlands. *Journal of Applied Ecology* 51: 289–298.
- Li, D., S. Chen, H. Lloyd, S. Zhu, K. Shan, and Z. Zhang. 2013. The importance of artificial habitats to migratory waterbirds within a natural/artificial wetland mosaic, Yellow River Delta, China. *Bird Conservation International* 23: 184–198.
- Liu, J., H. Xiao, F. Lei, Q. Zhu, K. Qin, X.-W. Zhang, X.-L. Zhang, D. Zhao, et al. 2005. Highly pathogenic H5N1 influenza virus infection in migratory birds. *Science* 309: 1206.
- Morin, C.W., B. Stoner-Duncan, K. Winker, M. Scotch, J.J. Hess, J.S. Meschke, K.L. Ebi, and P.M. Rabinowitz. 2018. Avian influenza virus ecology and evolution through a climatic lens. *Environment International* 119: 241–249.
- Muzaffar, S.B., J.Y. Takekawa, D.J. Prosser, S.H. Newman, and X. Xiao. 2010. Rice production systems and avian influenza: Interactions between mixed-farming systems, poultry and wild birds. Waterbirds 33: 219–230.
- National Bureau of Statistics. 2016. *Chinese national statistics*. China: Beijing.
- O'Donnell, M.J., S.L. Chin, S. Rangarajan, D. Xavier, L. Liu, H. Zhang, P. Rao-Melacini, X. Zhang, et al. 2016. Global and regional effects of potentially modifiable risk factors associated with acute stroke in 32 countries (INTERSTROKE): A case-control study. *The Lancet* 388: 761–775.
- Olsen, B., V.J. Munster, A. Wallensten, J. Waldenstrom, A.D.M.E. Osterhaus, and R.A.M. Fouchier. 2006. Global patterns of influenza A virus in wild birds. *Science* 312: 384–388.
- Pike, J., T. Bogich, S. Elwood, D.C. Finnoff, and P. Daszak. 2014. Economic optimization of a global strategy to address the pandemic threat. *Proceedings of the National Academy of Sciences* 111: 18519–18523.
- Poetri, O.N., M.V. Boven, I. Claassen, G. Koch, I.W. Wibawan, A. Stegeman, J. Van den Broek, and A. Bouma. 2014. Silent spread of highly pathogenic avian influenza H5N1 virus amongst vaccinated commercial layers. *Research in Veterinary Science* 97: 637–641.
- Prosser, D.J., L.L. Hungerford, R.M. Erwin, M.A. Ottinger, J.Y. Takekawa, and E.C. Ellis. 2013. Mapping avian influenza transmission risk at the interface of domestic poultry and wild birds. *Frontiers in Public Health* 1: 28.
- Railsback, S.F., and M.D. Johnson. 2014. Effects of land use on bird populations and pest control services on coffee farms. *Proceedings of the National Academy of Sciences* 111: 6109–6114.
- Ramsar Convention Secretariat. 2010a. Avian influenza and wetlands: Guidance on control of and responses to highly pathogenic avian influenza. Gland: Ramsar Convention Secretariat.
- Ramsar Convention Secretariat. 2010b. Managing wetlands: Frameworks for managing Ramsar Sites and other wetlands. Gland: Ramsar Convention Secretariat.

- Ramsar Convention Secretariat. 2019. *The Ramsar Sites Criteria*. Gland: The Ramsar Convention Secretariat.
- Schulz, K.F., and D.A. Grimes. 2002. Case-control studies: Research in reverse. *The lancet* 359: 431–434.
- Si, Y., W. de Boer, and P. Gong. 2013. Different environmental drivers of highly pathogenic avian influenza H5N1 outbreaks in poultry and wild birds. *PLoS ONE* 8: e53362.
- Si, Y., T. Wang, A.K. Skidmore, W.F. de Boer, L. Li, and H.H.T. Prins. 2010. Environmental factors influencing the spread of the highly pathogenic avian influenza H5N1 virus in wild birds in Europe. *Ecology and Society* 15: 26.
- Takekawa, J.Y., S.H. Newman, X. Xiao, D.J. Prosser, K.A. Spragens, E.C. Palm, B. Yan, T. Li, et al. 2010. Migration of waterfowl in the East Asian flyway and spatial relationship to HPAI H5N1 outbreaks. Avian Diseases 54: 466–476.
- Tian, H., S. Zhou, L. Dong, T.P. Van Boeckel, Y. Cui, Y. Wu, B. Cazelles, S. Huang, et al. 2015. Avian influenza H5N1 viral and bird migration networks in Asia. *Proceedings of the National Academy of Sciences* 112: 172–177.
- USDA Foreign Agricultural Service. 2017. China—Peoples Republic of Poultry and Products Semi-annual 2017 GAIN Report Number: CH17005. Washington DC: USDA Foreign Agricultural Service.
- Wang, Z., J. Wu, M. Madden, and D. Mao. 2012. China's wetlands: Conservation plans and policy impacts. Ambio 41: 782–786.
- Welte, V.R., and M.V. Teran. 2004. Emergency Prevention System (EMPRES) for transboundary animal and plant pests and diseases. The EMPRES-Livestock: An FAO initiative. Annals of the New York Academy of Sciences 1026: 19–31.
- Wilson, E.O. 2016. *Half-earth: Our planet's fight for life*. New York: WW Norton & Company.
- Wu, X., M. Lv, Z. Jin, R. Michishita, J. Chen, H. Tian, X. Tu, H. Zhao, et al. 2014. Normalized difference vegetation index dynamic and spatiotemporal distribution of migratory birds in the Poyang Lake wetland, China. *Ecological Indicators* 47: 219–230.
- Wu, T., and C. Perrings. 2017. Conservation, development and the management of infectious disease: Avian influenza in China, 2004–2012. Philosophical Transactions of the Royal Society B: Biological Sciences 372: 20160126.
- Xiao, X., S. H. Newman, T. McCracken, and C. Ding. 2010. Wild waterfowl—Domestic poultry—Human Interfaces An Integrated Pilot Study in Poyang Lake, Jiangxi, China. The 2nd international workshop on community-based data synthesis, analysis and modelling of highly pathogenic avian influenza H5N1 in Asia.
- Xu, W., Y. Xiao, J. Zhang, W. Yang, L. Zhang, V. Hull, Z. Wang, H. Zheng, et al. 2017. Strengthening protected areas for biodiversity and ecosystem services in China. *Proceedings of the National Academy of Sciences* 114: 1601–1606.
- Yan, D., U.A. Schneider, E. Schmid, H. Huang, L. Pan, and O. Dilly. 2013. Interactions between land use change, regional development, and climate change in the Poyang Lake district from 1985 to 2035. Agricultural Systems 119: 10–21.
- Yong, D.L., A. Jain, Y. Liu, M. Iqbal, C.Y. Choi, N.J. Crockford, S. Millington, and J. Provencher. 2018. Challenges and opportunities for transboundary conservation of migratory birds in the East Asian-Australasian flyway. *Conservation Biology* 32: 740–743.
- Yusuf, S., S. Hawken, S. Ôunpuu, T. Dans, A. Avezum, F. Lanas, M. McQueen, A. Budaj, et al. 2004. Effect of potentially modifiable risk factors associated with myocardial infarction in 52 countries (the INTERHEART study): Case-control study. *The Lancet* 364: 937–952.
- Zhang, Y., A.D. Fox, L. Cao, Q. Jia, C. Lu, H.H.T. Prins, and W.F. de Boer. 2019. Effects of ecological and anthropogenic factors on



waterbird abundance at a Ramsar Site in the Yangtze River Floodplain. *Ambio* 48: 293–303.

Zhang, Y., Q. Jia, H.H.T. Prins, L. Cao, and W. de Boer. 2015. Individual-area relationship best explains goose species density in wetlands. *PLoS ONE* 10: e0124972.

Zhang, L., X. Wang, J. Zhang, Z. Ouyang, S. Chan, M. Crosby, D. Watkins, J. Martinez, et al. 2017. Formulating a list of sites of waterbird conservation significance to contribute to China's Ecological Protection Red Line. *Bird Conservation International* 27: 153–166.

Zhang, Z., X. Wang, X. Zhao, B. Liu, L. Yi, L. Zuo, Q. Wen, F. Liu, et al. 2014. A 2010 update of national land use/cover database of China at 1:100000 scale using medium spatial resolution satellite images. *Remote Sensing of Environment* 149: 142–154.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

AUTHOR BIOGRAPHIES

Tong Wu (⋈) is a postdoctoral researcher at the Research Center for Eco-Environmental Sciences of the Chinese Academy of Sciences. His research interests include environmental health, environmental economics, and conservation biology.

Address: State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100875, China.

Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

e-mail: tongwu15@outlook.com

Charles Perrings is a Professor at the School of Life Sciences at Arizona State University. His research interests include environmental economics, ecological economics, and epidemiological economics.

Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

e-mail: Charles.Perrings@asu.edu

Chenwei Shang is a postdoctoral researcher at the Center for Human-Environment System Sustainability at Beijing Normal University. His research interests include landscape ecology and sustainability science. Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

Address: Center for Human-Environment System Sustainability (CHESS), State Key Laboratory of Earth Surface Processes and Resource Ecology (ESPRE), Beijing Normal University, Beijing 100875, China.

e-mail: cshang3@asu.edu

James P. Collins is a Professor at the School of Life Sciences at Arizona State University. His research interests include conservation biology, evolutionary ecology, and disease ecology.

Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

e-mail: jcollins@asu.edu

Peter Daszak is President of the EcoHealth Alliance. His research interests include disease ecology, conservation biology, and public health.

Address: EcoHealth Alliance, 460 West 34th Street - 17th Floor, New York, NY 10001, USA.

e-mail: daszak@ecohealthalliance.org

Ann Kinzig is a Professor at the School of Life Sciences at Arizona State University. Her research interests include ecology, ecological economics, and conservation biology.

Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

Address: Global Institute of Sustainability, Arizona State University, 800 South Cady Mall, Tempe, AZ 85287, USA.

e-mail: Ann.Kinzig@asu.edu

Ben A. Minteer is a Professor at the School of Life Sciences at Arizona State University. His research interests include environmental ethics, environmental history, and environmental policy.

Address: School of Life Sciences, Arizona State University, 427 East Tyler Mall, Tempe, AZ 85287, USA.

e-mail: Ben.Minteer@asu.edu

