Veterinary Record Open

OPEN ACCESS

Meteorological factors affecting the risk of transmission of HPAI in Miyazaki, Japan

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► Additional material is published online only. To view please visit the journal online (http://dx.doi.org/10.1136/vetreco-2019-000341).

To cite: Arikawa G, Fujii Y, Abe M, *et al*. Meteorological factors affecting the risk of transmission of HPAI in Miyazaki, Japan. *Veterinary Record Open* 2019;**6**:e000341. doi:10.1136/vetreco-2019-000341

Received 05 March 2019
Revised 25 June 2019
Accepted 19 August 2019

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ABSTRACT

Highly pathogenic avian influenza (HPAI) outbreaks engender a severe economic impact on the poultry industry and public health. Migratory waterfowl are considered the natural hosts of HPAI virus, and HPAI viruses are known to be transmitted over long distances during seasonal bird migration. Bird migration is greatly affected by the weather. Many studies have shown the relationship between either autumn or spring bird migration and climate. However, few studies have shown the relationship between annual bird migration and annual weather. This study aimed to establish a model for the number of migratory waterfowl involved in HPAI virus transmission based on meteorological data. From 136 species of waterfowl that were observed at Futatsudate in Miyazaki, Japan, from 2008 to 2016, we selected potential high-risk species that could introduce the HPAI virus into Miyazaki and defined them as 'risky birds'. We also performed cluster analysis to select meteorological factors. We then analysed the meteorological data and the total number of risky birds using a generalised linear mixed model. We selected 10 species as risky birds: Mallard (*Anas platyrhynchos*), Northern pintail (*Anas acuta*), Eurasian wigeon (*Anas penelope*), Eurasian teal (*Anas crecca*), Common pochard (*Aythya ferina*), Eurasian coot (*Fulica atra*), Northern shoveler (*Anas clypeata*), Common shelduck (*Tadorna tadorna*), Tufted duck (*Aythya fuligula*) and Herring gull (*Larus argentatus*). We succeeded in clustering 35 meteorological factors into four clusters and identified three meteorological factors associated with their migration: (1) the average daily maximum temperature; (2) the mean value of global solar radiation and (3) the maximum daily precipitation. We thus demonstrated the relationship between the number of risky birds and meteorological data. The dynamics of migratory waterfowl was relevant to the risk of an HPAI outbreak, and our data could contribute to cost and time savings in strengthening preventive measures against epidemics.

INTRODUCTION

Bird migration plays an important role in the transmission and dissemination of several infectious diseases including highly pathogenic avian influenza (HPAI), West Nile virus infection, Lyme disease and infections caused by enteropathogens.[1] In particular, HPAI is a threat to both animal health and public health.[2 3] Bird migration is an important risk factor in HPAI outbreaks,[4] and outbreaks have been reported in countries where many waterfowl migrate from breeding grounds. In Japan, HPAI outbreaks have occurred at intervals of several seasons (table 1). Over 46% of HPAI outbreaks in Japan, from 2004 to 2016, occurred in Miyazaki Prefecture in southern Japan between 30°21′39″ and 32°50′20″ N latitude and 130°42′12″ and 131°53′09″ E longitude (figure 1). HPAI outbreaks are associated with the arrival of migratory waterfowl, which are reservoirs of the HPAI virus.[1] The risk of HPAI outbreaks depends on the number of migratory waterfowl.[5–7] Therefore, it is important to understand the number and distribution of high-risk species (referred to here as 'risky birds'), which can, in turn, contribute to the implementation of efficient preventive measures.

Migration is a common feature of birds inhabiting seasonal environments.[8 9] Migration is essential for birds to survive in breeding grounds and overwintering areas. Bird migration is greatly affected by weather.[10] Migratory waterfowl depend on the existence of wetlands in breeding grounds and stopovers. In addition to food, water, and shelter, wetlands provide waterfowl with roosting, breeding, and stopover sites during migration.[11 12] Many studies on either spring or autumn migration and weather have been reported. However, few studies have addressed the relationship between annual bird migration and annual weather.

Understanding the relationship between the arrival of migratory waterfowl relevant to HPAI outbreaks and meteorological factors associated with the number of migratory waterfowl is important in the development of preventive measures against HPAI epidemics. These factors could also be used as predictive variables for efficient surveillance of HPAI.

Table 1 Highly pathogenic avian influenza outbreak cases among poultry in Japan (as of 31 March 2016)

Year	Month	Province	Species	Cases	Destroyed	Virus type
2004	January	Yamaguchi	Layer	1	34 640	H5N1
2004	February	Oita	Japanese bantam, domestic duck	1	14	H5N1
2004	February–March	Kyoto	Layer	2	240 000	H5N1
2007	January	Miyazaki	Broiler breeder, broiler	2	70 000	H5N1
2007	January	Okayama	Layer	1	12 000	H5N1
2007	February	Miyazaki	Layer	1	93 000	H5N1
2010	November	Shimane	Layer	1	20 000	H5N1
2011	January	Kagoshima	Layer	1	8600	H5N1
2011	January	Aichi	Layer	1	150 000	H5N1
2011	January	Miyazaki	Broiler breeder	1	10 200	H5N1
2011	January	Miyazaki	Layer	1	410 000	H5N1
2011	January	Miyazaki	Broiler	1	10 000	H5N1
2011	January	Miyazaki	Broiler	1	92 000	H5N1
2011	January	Miyazaki	Broiler breeder	1	6600	H5N1
2011	January	Miyazaki	Broiler	1	40 000	H5N1
2011	January	Miyazaki	Broiler	1	40 000	H5N1
2011	January	Miyazaki	Broiler	1	190 000	H5N1
2011	February	Aichi	Laying broiler breeder	1	17 500	H5N1
2011	February	Oita	Layer	1	10 000	H5N1
2011	February	Wakayama	Layer	1	120 000	H5N1
2011	February	Mie	Broiler	1	67 000	H5N1
2011	February	Mie	Layer	1	260 000	H5N1
2011	February	Miyazaki	Broiler	1	40 000	H5N1
2011	February	Miyazaki	Broiler	1	96 000	H5N1
2011	February	Miyazaki	Broiler	1	30 000	H5N1
2011	February	Miyazaki	Broiler	1	33 000	H5N1
2011	February	Miyazaki	Broiler	1	7500	H5N1
2011	February	Nara	Layer	1	100 000	H5N1
2011	March	Miyazaki	Broiler	1	30 000	H5N1
2011	March	Chiba	Layer	1	35 000	H5N1
2011	March	Chiba	Broiler	1	62 000	H5N1
2014	April	Kumamoto	Broiler	1	110 000	H5N8
2014	December	Miyazaki	Broiler	1	4000	H5N8
2014	December	Miyazaki	Broiler	1	42 000	H5N8
2014	December	Yamaguchi	Broiler	1	32 000	H5N8
2015	January	Okayama	Layer	1	200 000	H5N8
2015	January	Saga	Broiler	1	73 000	H5N8

Our study aimed to better understand the relationships between the migration of waterfowl and weather in Miyazaki Prefecture. We analysed statistical relationships between the total abundance of migratory waterfowl and the meteorological data over a 10-day period. By understanding the correlations between meteorological data and bird abundance, we aimed to develop predictive tools to identify patterns in migratory waterfowl abundance and the associated risk posed by HPAI.

MATERIALS AND METHODS

Data source for waterfowl migrating into Miyazaki

The number of migratory waterfowl is recorded during the migration period, from October to May every year, by the Ministry of Environment in Japan (http://www.env.go.jp/nature/dobutsu/bird_flu/migratory/ap_wr_transit/index.html). The Ministry of Environment in Japan conducts this observation three times a month (early, middle and late in the month) at 39 locations

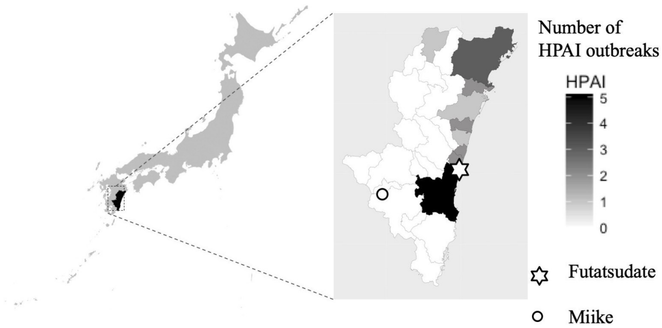

Figure 1 Location of Miyazaki Prefecture. Miyazaki is a prefecture of Japan located on the Eastern coast of Kyushu Island. Location of Futatsudate and Miike. Futatsudate (white hexagram) is located in the centre of the coastal area of Miyazaki City, at 32°03′37N latitude and 131°49′53 E longitude. Miike (white circle) is situated in the west area of Miyazaki Prefecture, at 31°72′355 latitude and 130°71′26 E longitude. HPAI, highly pathogenic avian influenza.

during the migration period. The purpose of this observation was to understand the tendency of migratory waterfowl species and the number of migratory waterfowl migrating to the wildlife sanctuary designated by the government during the migration period. Recently, these data have also been used to employ HPAI outbreak preventive measures by the government. These are open-source data that are updated monthly. In Japan, there are 39 observation locations, which include two points in Miyazaki: Futatsudate and Miike. In total, 18 HPAI outbreaks occurred in Miyazaki during the period spanning January 2004 through March 2016, with seven of these outbreaks occurring around Futatsudate (figure 1) and none occurring around Miike during this period. Therefore, we decided to use the data collected from the Futatsudate observation location.

The data for 186 terms (one term=10 days) for the period from October 2008 through March 2016, three observations per month, excluding the summer months of June through September, were included in our study. No data from June to September of each year were available because observations were not conducted during this time.

Selection of migratory waterfowl

Potential high-risk species were selected from all migratory waterfowl species observed at Futatsudate. The selection of migratory waterfowl was based on the criteria reported by the European Food Safety Agency[13] (figure 2). In this study, domestic poultry and migratory waterfowl that may be infected with HPAI virus of subtypes H5 and H7 fit the criteria of 'risky birds'. We assessed the distribution of the total number of risky birds and we used the total number of risky birds in one term as the data for subsequent statistical analysis.

Source of meteorological data

Open-source meteorological information is made available by the Japan Meteorological Agency (http://www.data.jma.go.jp/gmd/risk/obsdl/index.php). Meteorological factors such as atmospheric pressure, temperature, humidity, wind speed, precipitation, snow depth, sunshine hours, solar radiation, clouds, visibility and atmospheric phenomena are observed by weather stations. Among these, precipitation, wind speed, temperature and sunshine time are also recorded by the Automated Meteorological Data Acquisition System (AMeDAS). These data are updated daily. In Japan, there are about 60 weather stations and about 1300 AMeDAS (http://www.jma.go.jp/jma/kishou/know/chijyou/surf.html; http://www.jma.go.jp/jma/kishou/know/amedas/kaisetsu.html). We used the data from 186 terms for 10 days per month (early, middle and late in the month), for 35 factors of meteorological information observed at the Miyazaki local weather station, from October 2008 through March 2016 (table 2), as this is the nearest local weather station to Futatsudate.

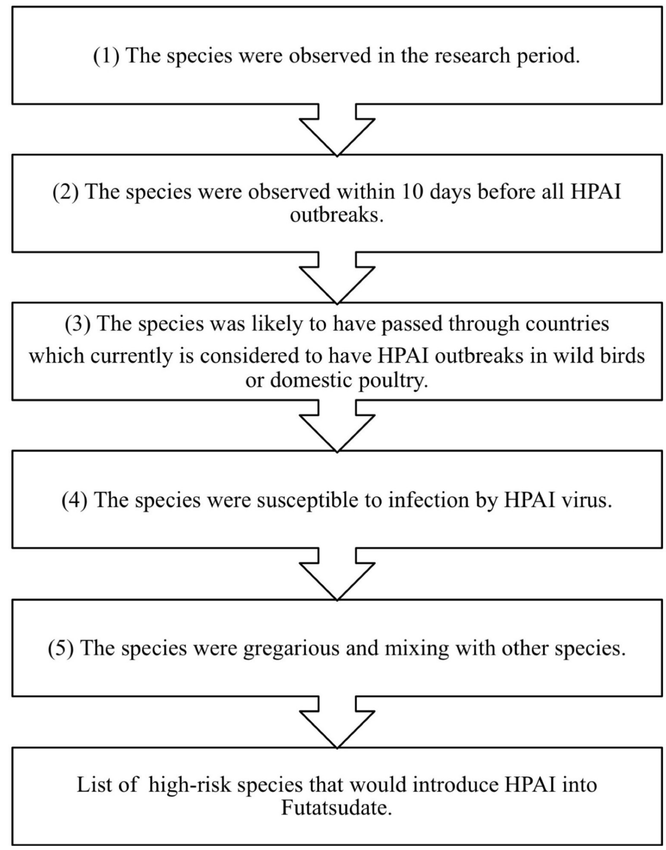

Figure 2 Decision tree for the selection of migratory waterfowl most likely to introduce highly pathogenic avian influenza (HPAI) into Miyazaki. One hundred and thirty-six species were checked according to the first criteria. If any species met the first criteria, they were checked for the next criteria. Finally, we considered the species that met all criteria as risky birds.

Cluster analysis for meteorological data

Cluster analysis groups objects based on the information found in the data describing the objects or their relationships. To prevent overfitting in our models by too many meteorological factors, we narrowed down the

Table 2 Definition of meteorological factors

Meteorological factors	Acronyms	Unit	Definition	Period	Data source
Average of daily mean temperature	Temp1	°C	Average of daily mean temperature on certain 10 days	October 2008–March 2016 (excluding every June–September)	Japan Meteorological Agency
Days of daily minimum temperature under 0°C	Temp2	Day	The days with less than 0°C of daily minimum temperature on certain 10 days		
Days of daily maximum temperature over 25°C	Temp3	Day	The days with more than 25°C of daily maximum temperature on certain 10 days		
Days of daily mean temperature over 25°C	Temp4	Day	The days with more than 25°C of daily mean temperature on certain 10 days		
Average of daily maximum temperature	Temp5	°C	Average of daily maximum temperature on certain 10 days		
Average of daily minimum temperature	Temp6	°C	Average of daily minimum temperature on certain 10 days		
Maximum temperature	Temp7	°C	The maximum temperature on certain 10 days		
Minimum temperature	Temp8	°C	The minimum temperature on certain 10 days		
Minimum of daily maximum temperature	Temp9	°C	The minimum of daily maximum temperature on certain 10 days		
Maximum of daily minimum temperature	Temp10	°C	The maximum of daily minimum temperature on certain 10 days		
Total precipitation	Rain1	mm	Sum of precipitation on certain 10 days		
Maximum precipitation for 1 hour	Rain2	mm	Maximum precipitation for 1 hour on certain 10 days		
Maximum daily precipitation	Rain3	mm	Maximum daily precipitation on certain 10 days		
Days of daily precipitation over 1 mm	Rain4	Day	The days with over 1 mm of daily precipitation on certain 10 days	October 2008–March 2016 (excluding every June–September)	Japan Meteorological Agency
Hours of daylight	Sunshine1	Hour	Sum of hours with quantity of direct solar radiation more than 0.12 kW/m^2 on certain 10 days		
Percentage of sunshine	Sunshine2	%	Percentage of sunshine on certain 10 days		
Days with daily hours of daylight of under 0.1 hour	Sunshine3	Day	The days with under 0.1 hours of daily hours of daylight on certain 10 days		
Days with daily sunshine rate of over 40%	Sunshine4	Day	The days with over 40% of daily sunshine rate on certain 10 days		

Continued

Table 2 Continued

Meteorological factors	Acronyms	Unit	Definition	Period	Data source
Mean value of global solar radiation	Sunshine5	MJ/m^2	Average of daily mean value of global solar radiation on certain 10 days		
Mean wind speed	Wind1	m/s	Average of daily mean wind speed on certain 10 days		
Maximum wind speed	Wind2	m/s	The maximum of the wind velocity mean for 10 minutes on certain 10 days		
Days of daily maximum wind speed over 10 m/s	Wind3	Day	The days with over 10 m/s of daily maximum wind speed on certain 10 days		
Maximum instantaneous wind speed	Wind4	m/s	The maximum of the instantaneous wind speed on certain 10 days		
Average vapour pressure	Humidity1	hPa	Average vapour pressure on certain 10 days		
Mean relative humidity	Humidity2	%	Average of daily mean humidity on certain 10 days		
Minimum relative humidity	Humidity3	%	The minimum of the ratio of the partial pressure of water vapour to the equilibrium vapour pressure of water at a given temperature on certain 10 days	October 2008–March 2016 (excluding every June–September)	Japan Meteorological Agency
Mean station pressure	Press1	hPa	Average of the atmospheric pressure computed using station elevation as the reference datum level on certain 10 days		
Mean sea level pressure	Press2	hPa	Average of the atmospheric pressure at sea level at a given location on certain 10 days		
Minimum sea level pressure	Press3	hPa	Minimum of the atmospheric pressure at sea level at a given location on certain 10 days		
Average percentage of cloud amount	Cloud1	%	Average percentage of cloud amount on certain 10 days		
Minimum sea level pressure	Press3	hPa	Minimum of the atmospheric pressure at sea level at a given location on certain 10 days		
Average percentage of cloud amount	Cloud1	%	Average percentage of cloud amount on certain 10 days		
Days of daily cloud amount over 8.5	Cloud2	Day	The days with daily cloud amount over 8.5 on certain 10 days		
Days of daily cloud amount under 1.5	Cloud3	Day	The days with daily cloud amount under 1.5 on certain 10 days		
Days with fogging	Fog	Day	The days with fog on certain 10 days		
Days with thundering	Thunder	Day	The days with thunder on certain 10 days		
Days with snowing	Snow	Day	The days with snow on certain 10 days	October 2008–March 2016 (excluding every June–September)	Japan Meteorological Agency

meteorological factors by cluster analysis. In this study, we performed hierarchical cluster analysis using Ward's method.[14] Ward's method is a criterion using the error sum of squares as the objective function applied in hierarchical cluster analysis.[14]

Relationship between weather and waterfowl abundance

We totalled the number of selected risky birds for each term and examined the distribution of the total number of risky birds for subsequent analysis. We analysed meteorological data and the total number of risky birds using generalised linear mixed models. For analysis of the generalised linear mixed model fitted in R, we used the lme4 package. We used 'year' as the random effect for the generalised linear mixed model. The model is described as follows:

$$\text{logit}\ (\text{RB}) = \log\ (\text{RB}/1 - \text{RB})) = \alpha + \sum \beta\chi + \text{RY} + \text{e}$$

where RB represents the total number of risky birds, α is the model intercept, χ is the fixed effects with $p<0.05$ in the univariate analyses, β is its coefficient, RY is the random year effect and e is the residual term of the Poisson distribution. The best model was constructed by a stepwise approach, observing the changes in Akaike's Information Criterion (AIC) of each model. The final model was obtained with the minimum AIC and $p<0.05$ for the remaining fixed effects. Multicollinearity was evaluated using the variance inflation factor.[15,16] All statistical analyses were conducted using R software V.3.2.1 (R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/).

Analysis of the correlation between our model and the measured values

To calculate the predicted value for each term using our model, three types of meteorological data for the term—average daily maximum temperature, mean value of global solar radiation and maximum daily precipitation—were substituted into the obtained model. Spearman's rank correlation coefficient was used for comparison between the predicted value and the measured value for each term.

Prediction of the total number of risky birds by our model

To predict the total number of risky birds from October 2016 through May 2019 using our model, three types of meteorological data, that is, average daily maximum temperature, mean value of global solar radiation and maximum daily precipitation, were substituted into the obtained model. Spearman's rank correlation coefficient was used for comparison between the predicted value and the measured value for each term.

RESULTS

Selection of migratory waterfowl

Ten risky bird species were chosen from 136 species of migratory waterfowl observed at Futatsudate from

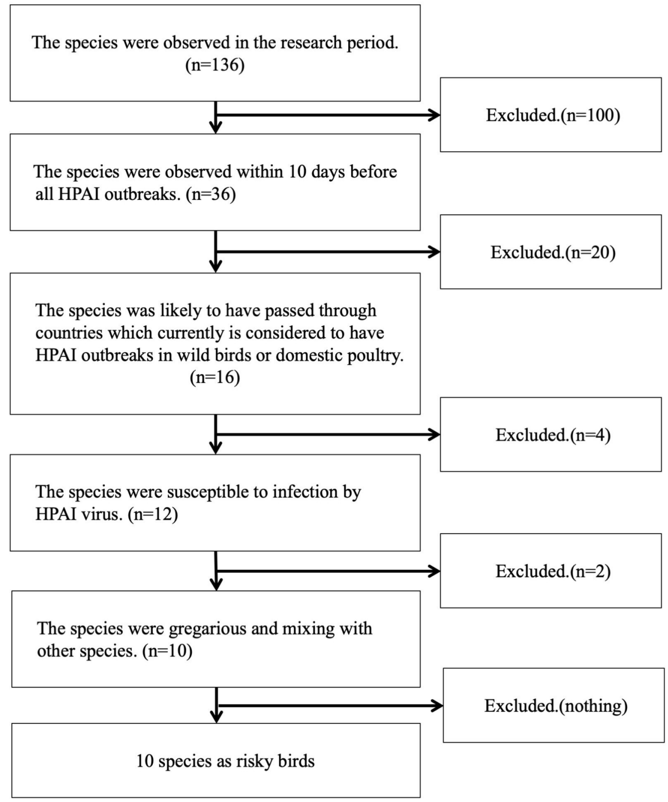

Figure 3 Results of the selection process for risky birds.

October 2008 through March 2016 (online supplementary file 1). The 10 selected waterfowl species considered as risky birds (selected as detailed in figure 3) were as follows: Mallard (*Anas platyrhynchos*), Northern pintail (*Anas acuta*), Eurasian wigeon (*Anas penelope*), Eurasian teal (*Anas crecca*), Common pochard (*Aythya ferina*), Eurasian coot (*Fulica atra*), Northern shoveler (*Anas clypeata*), Common shelduck (*Tadorna tadorna*), Tufted duck (*Aythya fuligula*) and Herring gull (*Larus argentatus*).

The total number of risky birds was distributed according to Poisson distribution.

Cluster analysis of the meteorological data

As a result of cluster analysis, meteorological factors were divided into four clusters (figure 4). One cluster contained meteorological factors related to temperature and atmospheric pressure. Another cluster contained meteorological factors related to wind and snow. The third cluster contained meteorological factors related to rain. The last cluster contained meteorological factors related to sunshine, cloud, and the remaining other meteorological factors.

Relationship between weather and waterfowl abundance

As a result of the generalised linear mixed model, we could estimate the total number of risky birds by three meteorological factors (table 3). The results of univariable analysis of other competing meteorological factors are presented in the online supplementary file 2.

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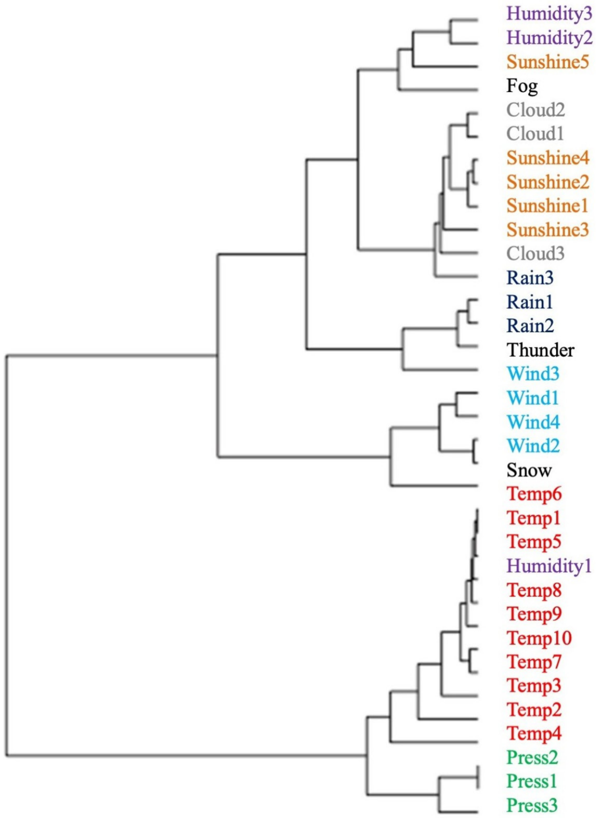

Figure 4 Results of cluster analysis.

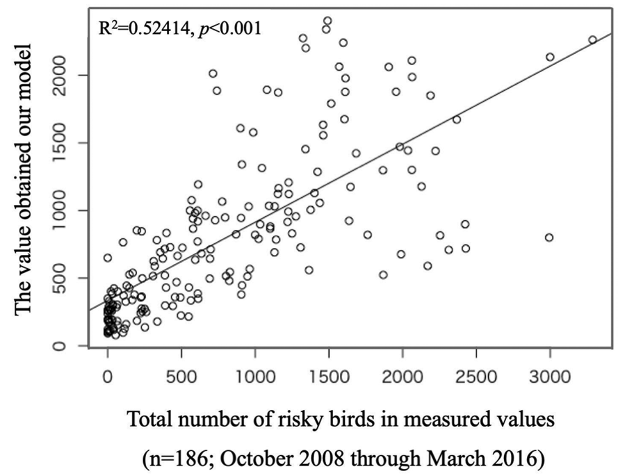

Figure 5 Scatter plot between the predicted values and the measured values, and the regression line (October 2008–March 2016).

Analysis of the correlation between our model and the measured values

The scatter plot of predicted values and measured values showing the regression line is presented in figure 5. The coefficient of determination between the predicted values and the measured values was 0.52414 (p<0.001).

Prediction of the total number of risky birds by our model

The scatter plot of predicted values and measured values showing the regression line is presented in figure 6. The coefficient of determination between the predicted values and the measured values was 0.5577 (p<0.001).

DISCUSSION

The relationship between the number of HPAI risky migratory waterfowl arriving in Miyazaki and local meteorological data was assessed using generalised lined mixed modelling and open-source data for 186 terms in Miyazaki, Japan. We selected 10 species of risky birds that were most likely to introduce HPAI virus into Miyazaki from 136 species. The migration of these 10 species of risky birds into Miyazaki showed a significant correlation with three meteorological factors. Predicting the number of migratory waterfowl can contribute to efficient preventive measures for infectious diseases derived from these migratory waterfowl. Our study selected 10 species of wild birds including eight species of the order Anseriformes, one species of the order Gruiformes and one species of the order Charadriiformes as risky birds. These risky birds have been previously reported as species at risk of introducing HPAI into several countries in Europe, America, and Asia.[13 17–20]

We succeeded in identifying three meteorological factors associated with the migration of risky birds. First, there was a significantly inverse relationship between the average daily maximum temperature and the number of risky birds. Low temperatures in autumn encourage migratory waterfowl to migrate southwards over winter.[21] In a low temperature environment, it is difficult for birds to find food and water because plants cannot grow and water bodies freeze. Additionally, severe weather conditions, especially low temperatures, are known to cause stress in birds.[22–27] Thus, in autumn, birds leave their breeding grounds and migrate to a relatively warmer wintering ground at lower latitude to survive. Wintering

Table 3 Results of the generalised linear mixed model for the relationship between meteorological factors and the total number of migratory waterfowl

	Fixed effects				Random effects	
Parameters	Estimate	SE	z value	Pr(>|z|)	Variance	SD
(Intercept)	9.571	0.123	77.58	<0.001	0.1204	0.347
Average of daily maximum temperature	−0.084	0.0007	−109.25	<0.001		
Mean value of global solar radiation	−0.004	0.0001	−34.46	<0.001		
Maximum daily precipitation	−0.116	0.001	−113.56	<0.001		

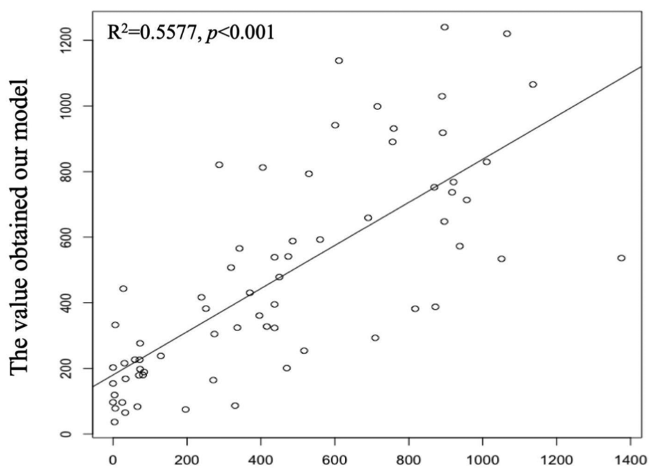

Figure 6 Scatter plot between the predicted values and the measured values, and the regression line (October 2016–May 2019).

grounds for the birds, including Japan, are located at a lower latitude than their breeding grounds, such as Siberia and Mongolia. This is why the number of migratory waterfowl increases in Japan in that season. For the above reasons, air temperature and the number of risky birds showed a significantly inverse relationship in our study. Second, there was a significant direct relationship between the number of days with the mean value of global solar radiation and the number of risky birds. The climate in Miyazaki generally results in clear skies and little cloud. Sunshine affects the migration and distribution of waterfowl[28–30] and plant growth.[30] Birds often gather in sunny areas such as Qinghai Lake[31] in search of areas with abundant plants. Miyazaki also generally experiences a lot of strong sunshine. These facts are likely reasons for the increase in the number of migratory waterfowl in Miyazaki during the winter. Third, there was a significant direct relationship between the days with maximum daily precipitation and the number of risky birds. In previous studies, rain was the most consistent meteorological factor explaining variations in migration densities.[32 33] Furthermore, one study reported that few birds fly during rain.[34] These reports support our findings. To our knowledge, cluster analysis of meteorological factors has not been reported, although one previous study performed cluster analysis of the climate zone for domestic instead of meteorological factors.[35]

In Japan, every autumn when migratory waterfowl arrive, administrative organisations such as national and local governments strengthen measures to prevent HPAI outbreaks and the spread of infectious diseases. Concrete preventive measures include: (1) repairing poultry houses so that waterfowl and small animals cannot invade the poultry houses; (2) improving the hygiene of the environment around poultry houses so as not to attract waterfowl; (3) monitoring people and vehicles entering and exiting the poultry houses; (4) early detection and early reporting; (5) preparation of personnel and prevention materials in advance and (6) establishment of a network between relevant organisations. Some local governments continue to strengthen preventive measures from October through April. However, the administrative burden on local government and poultry farmers is significant. In Miyazaki, when the total number of risky birds during an HPAI outbreak and at other times was compared, the minimum value of the total number of risky birds during an HPAI outbreak was 398.0 and the median value was 748.5, whereas the corresponding values at other times were 0.0 and 592.0, respectively. If the minimum value of the total number of risky birds during a past HPAI outbreak in Miyazaki was taken as the cut-off value for epidemic prevention reinforcement, it would enable us to shorten the duration of epidemic prevention reinforcement by 34% from October through to April. This would reduce the burden of epidemic prevention. In addition, in Japan, about 15 000 samples per year (about US$10 per sample) are regularly inspected for HPAI; therefore, using our approach, US$50 000 might be saved in HPAI monitoring costs. Furthermore, if the minimum value was taken as the cut-off value for epidemic prevention reinforcement, the riskiest month would be predicted to be February. In February, 32 out of 33 terms (93.9%) over the period October 2008–May 2019 exceeded 398, which is the minimum value. If it was possible to predict the number of migratory waterfowl expected to arrive in the next month based on weather forecasts, administrative organisations would be able to encourage poultry farmers to employ strict biosecurity and preventive measures in advance. If developed, our technology could potentially be used to predict the number of migratory waterfowl before their arrival. This would make it possible to switch from cumbersome and diffuse preventive measures to more targeted strategies.

Observations of both meteorological data and waterfowl data are conducted in many countries. Our approach would be applicable to neighbouring areas in Japan, as well as neighbouring countries and beyond. Our approach can predict the number of migratory waterfowl using only open-source data available on the internet without the need to watch and count birds, which requires manpower and expertise (eg, in distinguishing bird species and in counting groups of birds). In this study, meteorological factors influencing the migration of waterfowl were identified. However, even though similar weather conditions were recorded across Miyazaki Prefecture, containing a stopover site for migratory waterfowl, there were differences in the occurrence of HPAI outbreaks. Using our method, we can predict more than 50% of the total number of risky birds using only local meteorological data. This percentage could potentially be increased by considering various other factors. For example, geographical factors such as the number and size of nearby lakes, environmental factors (such as starvation and drought occurrence) in breeding areas and meteorological factors in breeding areas, could also be considered. In future studies, we intend to expand our method by conducting spatial analysis. We suggest that this approach can be applied globally to predict periods of high risk of HPAI outbreak in specific areas.

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Acknowledgements We thank Naoaki Misawa, Yoshitaka Goto, Nariaki Nonaka, Tamaki Okabayashi and Shinji Watanabe for comments and suggestions that helped improve the research. We thank Kate Fox, DPhil, from Edanz Group (www.edanzediting.com/ac) for editing a draft of this manuscript.

Contributors GA designed the study and wrote the initial draft of the manuscript. SS contributed to analysis and interpretation of data and assisted in manuscript preparation. All other authors contributed to critically reviewing the manuscript, approved the final version of the manuscript and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Funding The authors have not declared a specific grant for this research from any funding agency in the public, commercial or not-for-profit sectors.

Competing interests None declared.

Patient consent for publication Not required.

Provenance and peer review Not commissioned; externally peer reviewed.

Data availability statement The data that support the findings of this study are openly available at http://www.env.go.jp/nature/dobutsu/bird_flu/migratory/ap_wr_transit/index.html

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