

1 Title: Synchrony of Bird Migration with Avian Influenza Global Spread;
2 Implications for Vulnerable Bird Orders

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Abstract

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Highly pathogenic avian influenza virus (HPAIV) A H5 clade 2.3.4.4 has caused worldwide outbreaks in domestic poultry, occasional spillover to humans, and increasing deaths of diverse species of wild birds since 2014. Wild bird migration is currently acknowledged as an important ecological process contributing to the global dispersal of HPAIV H5. However, it is unclear *how seasonal bird migration facilitates global virus dispersal, and which avian species are exposed to HPAI H5 clade 2.3.4.4 viruses and where*. To shed light on ongoing global outbreaks, we sought to explore these questions through phylodynamic analyses based on empirical data of bird movement tracking and virus genome sequences. First, based on viral phylogeography and bird migration networks, we demonstrate that seasonal bird migration can explain salient features of the global dispersal of clade 2.3.4.4. Second, we detect synchrony between the seasonality of bird annual cycle phases and virus lineage movements. We reveal the differing vulnerable bird orders at geographical origins and destinations of HPAIV H5 lineage movements. Notably, we highlight the potential importance of relatively under-discussed Suliformes and Ciconiiformes, in addition to Anseriformes and Charadriiformes, in virus lineage movements. Our study provides a phylodynamic framework that links the bird movement ecology and genomic epidemiology of avian influenza; it highlights the importance of integrating bird behaviour and life history in avian influenza studies.

53 1 Introduction

54 The re-emergence of highly pathogenic avian influenza viruses (HPAIVs) subtype H5
55 clade 2.3.4.4 since 2014 [1] has caused unprecedentedly large numbers of wild bird deaths
56 worldwide [2]. In contrast to previous clades of the A/goose/Guangdong/1996 (Gs/GD)
57 lineage, there have also been more persistent spillovers to local domestic poultry [3–7], im-
58 pacting the poultry farming industry. Despite no onward human-to-human transmission
59 to date, occurrences of zoonotic jumps to humans pose potential threats to public health
60 [8–12]. The unique epidemiological pattern of clade 2.3.4.4 HPAIV H5 is potentially
61 shaped by eco-evolutionary processes: i) the continued selection for both higher trans-
62 missibility and virulence, e.g., as observed in ducks [13, 14]; ii) the interaction between
63 the viruses and a wider range of hosts [15].

64 To shed light on the underlying eco-evolutionary processes, it is critical to understand
65 the spatial dynamics of clade 2.3.4.4 and the ecological factors that influence these pat-
66 terns. Plausible ecological mechanisms for the global movement of HPAIVs include the
67 live poultry trade and wild bird migration [16, 17]. Preceding the recent re-emergence
68 of clade 2.3.4.4, there has been a long-term debate about whether wild bird migration
69 drives HPAIV dispersal [18, 19]. However, the re-emergence of clade 2.3.4.4 continues
70 to provide virological, epidemiological, and ecological evidence in support of the critical
71 role of migratory wild birds in HPAIV spread and evolution at a global scale. Com-
72 pared to previous clades, clade 2.3.4.4a during 2014/15 outbreaks was less pathogenic to
73 some species while being more effectively transmitted [20–22], possibly enabling infected
74 birds to migrate between continents. Subsequent phylodynamic work confirmed that the
75 introduction of clade 2.3.4.4a into Europe and North America was most likely via long-
76 distance flights of infected migratory birds [23]. During the 2016/17 outbreaks, the major
77 circulating clade 2.3.4.4b was more transmissible [24] and more virulent [14], related to
78 multiple internal genes [14, 24] and potentially their frequent reassortments [4–6]. Later
79 phylogenetic analysis showed a clear link between the reassortments and migratory birds,
80 as most reassorted gene segments were from migratory wild birds and originated at dates
81 and locations that corresponded to their hosts’ migratory cycles [25]. Integrating host
82 movement in studying HPAIV dispersal is important while challenging. One challenge
83 is insufficient bird movement data, which causes that previous global-scale studies [23]
84 cannot account for the high variation in bird behaviours across species and locations.

85 Another challenge of studying HPAIV dispersal in wild birds is the lack of HPAIV
86 prevalence data. Only a few studies document longitudinal HPAIV prevalence in wild bird
87 populations [26]. Compared to HPAIV, low pathogenic AIV (LPAIV) has better long-term
88 surveillance of infections or seroprevalence and related avian host ecology in disparate

89 bird habitats, e.g., the United States Geological Survey (USGS) surveillance of birds in
90 Alaska [27]. While longitudinal records provide insights into the role of life history and
91 ecology of local bird communities in LPAIV circulation[28], their conclusions are limited
92 to local dynamics and cannot be easily generalized. To resolve this challenge, ideally, we
93 should have systematic global surveillance for HPAIV. However, this is impossible due to
94 resource constraints.

95 Instead, we could design effective surveillance strategies by identifying vulnerable
96 avian species and high-risk geographical regions. Recently, researchers have addressed
97 these questions at a higher taxonomic level to include more diverse species. For example,
98 Hill et al. compared the different roles of species within the Anseriformes and Charadri-
99 iformes in the dispersal and spillover of AIVs [29]. They concluded that wild geese and
100 swans are the main source species of HPAIV H5, while gulls spread the viruses most
101 rapidly. Hicks et al. found that the inter-species transmission of AIVs in North Amer-
102 ica is positively associated with the overlap of habitats, suggesting the importance of
103 local bird community diversity [30]. However, they did not use empirical bird movement
104 data. Furthermore, given the heterogeneous biogeographical pattern of bird migrations,
105 identifying geographical hotspots requires linking global and local scales.

106 To fill this gap, we here focus on two questions related to the contributions of birds,
107 locally and globally, to the spatiotemporal dynamics of HPAIV H5 viruses; specifically,
108 i) how does seasonal bird migration facilitate global virus dispersal and ii) which avian
109 species are exposed to HPAIV H5 and where? To explore these questions, we first il-
110 lustrate the global circulation history of clade 2.3.4.4 using time-scaled phylogeographic
111 analyses of hemagglutinin (HA) genes of HPAIVs sampled from wild birds and poultry
112 between 2007 and 2018. ~~Building upon previous evidence, we propose possible routes of~~
113 ~~long-distance virus dispersal.~~ There are two caveats: first, while we only included HA,
114 internal genes also contribute to virus evolution, e.g., via reassortment [25]; second, the
115 geographical bias of virus sampling has a strong impact on the virus lineage movement
116 routes, especially for locations under-sampled. Based on ~~the estimated routes and~~ in-
117 ferred virus dispersal history, we quantify the contribution of seasonal bird migrations to
118 global virus dispersal and evolution. Second, we model the monthly geographical distri-
119 bution of bird orders using species distribution models based on environmental factors
120 and bird tracking data. We evaluate the risks of bird orders being exposed to HPAIV
121 H5 at geographical origins and destinations of virus lineage movement by analyzing the
122 statistical association of local bird distributions and virus lineage migration. Our study
123 provides an approach that integrates bird migration ecology in HPAIV epidemiological
124 studies to disentangle the mechanisms of interaction between HPAIV and wild birds.

125 2 Results

126 2.1 Seasonal bird migration associates with global HPAIV H5 127 dispersal

128 *Is the wide geographical range of HPAIV H5 clade 2.3.4.4 caused by frequent introductions*
129 *from one region to another, or a single introduction resulting in subsequent spread within*
130 *the area?* The discrete-trait phylogeographical analysis of HA genes exhibits scarce virus
131 lineage movements between aggregated regions, most of which are unidirectional (Figure
132 1A). It suggests that inter-regional viral introductions over long geographical distance oc-
133 cur at low frequency and in one direction. Furthermore, the sequences are highly clustered
134 by region, implying viral persistence within each region after introduction. These pat-
135 terns qualitatively match bird migration patterns: migratory birds can fly long distances
136 during their migrations, and only fly in one direction in a given season. After arriving
137 at stopover, breeding, or wintering sites, they usually stay for some time, allowing viral
138 transmission to other species or the environment.

139 To test quantitatively whether seasonal bird migration is a key predictor of HPAIV H5
140 dispersal, we fit a generalized linear model (GLM) parameterization of the discrete phylo-
141 geography using a Bayesian model selection procedure [31, 32]. Concurrently, we consider
142 seasonal bird migration, live poultry trade and poultry population size as covariates of
143 the diffusion rates between regions. To incorporate the potential seasonal difference in
144 viral dispersal, we model a time-heterogeneous phylogenetic history [33] with three sea-
145 sons based on bird annual cycle in North Hemisphere: non-migration (mid-November to
146 mid-February, mid-May to mid-September), spring migration (mid-February to mid-May)
147 and fall migration (mid-September to mid-November). Figure 1B shows the posterior es-
148 timates of the inclusion probabilities and conditional effect sizes (on a log scale) of the
149 covariates. It reveals that seasonal bird migration is the dominant driver of the global
150 virus lineage movements of HPAIV H5. This is shown in both the log conditional effect
151 size of the seasonal bird migration (mean: ~ 1.96 ; 95% highest probability density inter-
152 val, HPDI: 0.88-4.56) and the statistical support for its inclusion (posterior probability
153 > 0.999 and Bayes factor > 16565).

154 In contrast, poultry population size and the live poultry trade are not associated with
155 the inter-region dispersal of HPAIV H5 (Figure 1B) in this analysis. It is also evident in
156 both the effect size and the statistical support, e.g, the log conditional effect size of live
157 poultry trade (mean: ~ 0.44 , HPDI: 0.12-0.84) and the statistical support for its inclusion
158 (posterior probability: ~ 0.31 and Bayes factor: 5). To maintain genetic diversity in our
159 data set, we did not down-sample the sequences, which leaves considerable heterogeneity

160 in sample sizes among locations. Therefore, we included the sample size as a predictor
161 in the model to raise the credibility that the inclusion of other predictors is not due to
162 sampling bias. Based on these results, we used subsequent analyses to understand the
163 importance of different bird species at order taxonomy level in the global dispersal and
164 local emergence of HPAIV H5 clade 2.3.4.4.

165 **2.2 Vulnerable migratory bird orders at origin and destination** 166 **regions of HPAIV H5 virus lineage movement**

167 We identified 20 virus dispersal routes (Bayes factor >3) between the aggregated regions
168 in the Northern Hemisphere (Figure 2A) using the previous phylogeography analyses.
169 Seasonality is reflected in northward and southward virus lineage movements. Further-
170 more, it overlaps well with the bird migration seasonality. Most virus lineage movements
171 (14 of 20) show a single temporal peak (Figure S5, 2A). The peaks of the northward
172 routes overlap with spring bird migration and/or wintering period (upper rows of Fig-
173 ure 2A, Figure S5.1). Only one route (Japan-Korea to USA-Canada) overlaps with the
174 summer breeding period. Most southward virus lineage movements peak during the Fall
175 bird migration period, although some peaks continue in November when birds might still
176 be migrating along some routes (lower half of Figure 2A, Figure S5.2). Only one route
177 (Europe to Qinghai) overlaps with the wintering period. In summary, in the North-
178 ern Hemisphere, virus lineage movements from south to north occur mainly during the
179 wintering period and spring bird migration, while southward virus lineage movements
180 occur mainly during the fall migration period when birds fly to the south. This as-
181 sociation of seasonality in bird migration and HPAIV H5 lineage movement suggests
182 that bird migration is a mechanism of HPAIV H5 global dispersal. It also implies that
183 breeding grounds are potential genetic pools of HPAIV H5 diversity for southward virus
184 lineage movements associated with bird migration; wintering grounds play a similar role
185 for the northward viral lineage movements. Additionally, the results show more virus
186 lineage movements during the fall migration (Southward Markov Jump counts: 310498
187 per month, September-November) than the spring migration (Northward Markov Jump
188 counts: 257503 per month, March-May). Virus lineage movements also have higher
189 relative frequency during the fall migration (shown in the higher peak in Figure 2). In-
190 terestingly, birds also migrate in a larger abundance in the fall than during spring, as the
191 population size becomes larger after breeding.

192 *Which migratory bird orders might be exposed to HPAIV H5 at the origin or desti-*
193 *nation regions of virus lineage movements?* To explore this question, we examined the
194 synchrony of bird order distribution and virus lineage movements. The result shows that

195 8 bird orders (out of 9) at origin or destination regions are correlated with 12 virus lin-
196 eage movement routes (out of 20) (Table S4, Figure 2A). Notably, the distribution of
197 Suliformes, e.g., cormorants, during a year in Europe ($r = 0.996$, 95% confidence inter-
198 vals, CI: [-0.566, 0.566], $p < 0.001$) and Qinghai ($r = 0.899$, CI: [-0.566, 0.566], $p < 0.002$)
199 synchronizes with virus lineage movements from Europe to Qinghai, suggesting that Suli-
200 formes might be associated with HPAIV H5 spread from Europe to Qinghai. However,
201 due to the possible under-sampling of viruses in northern and central Eurasia, we can-
202 not conclude that virus lineage movements occur directly from Europe to Qinghai. In
203 addition, Suliformes, along with Charadriiformes, Ciconiiformes, and Anseriformes, are
204 associated with multiple (>2) virus lineage movements. Three routes of virus lineage
205 movement are related to the distribution of multiple (>2) bird orders:

- 206 • The virus lineage movement from Qinghai to Europe is associated with the Charadri-
207 iformes distribution in Qinghai ($r = -0.820$, $p < 0.005$), and the distribution of
208 Suliformes ($r = 0.924$, $p < 0.001$) and Passeriformes ($r = 0.878$, $p < 0.002$) in
209 Europe.
- 210 • The virus lineage movement from South China to South East Asia synchronizes with
211 the Charadriiformes distribution in South China ($r = 0.803$, $p < 0.005$), and the
212 distribution of Suliformes ($r = 0.912$, $p < 0.002$) and Falconiformes ($r = 0.890$, $p <$
213 0.002) in South East Asia.
- 214 • The virus lineage movement from Europe to Africa is related to the Ciconiiformes
215 distribution in Europe ($r = 0.813$, $p < 0.005$), and the distribution of Charadri-
216 iformes ($r = 0.886$, $p < 0.002$) and Anseriformes in Africa ($r = 0.905$, $p < 0.002$).

217 Despite the possible geographical sampling bias, our results suggest integrating host dis-
218 tribution inference and phylogeographic analysis might be able to retrospectively identify
219 important bird species and geographical regions in avian influenza transmission.

220 3 Discussion

221 Here, we report a phylodynamic analysis linking spatial ecology of avian hosts and HPAIV
222 H5 virus lineage movements. Our results support previous findings on the important
223 role of bird migration in the dissemination of HPAIV H5 clade 2.3.4.4 [23]. We found
224 that the seasonal wild bird migration network is associated with the global diffusion
225 and evolutionary dynamics of HPAIV H5. A previous study found that the 2014/2015
226 outbreaks of HPAIV H5 in Europe and North America were likely introduced by wild
227 bird migration [23] by comparing the inferred ancestral host-type and location traits of

228 the viral genome sequences [23]. Our study advances this finding by directly integrating
229 the bird migration trajectory network into the virus phylogeographic reconstruction. In
230 addition, we found that inter-regional live poultry trade is not associated with the global
231 HPAIV H5 dispersal, consistent with previous studies [16, 23]. The same previous study
232 found that the international poultry trade's direction is opposite to the global spread
233 direction of HPAIV H5 clade 2.3.4.4 [23]. Another previous study demonstrated large-
234 scale H5N1 transmission dynamics are structured according to different bird flyways and
235 driven by the Anatidae family, while the Phasianidae family, largely representing poultry,
236 is an evolutionary sink [16].

237 Historically, Anseriformes have been the focus of wild bird hosts when studying host-
238 pathogen interaction in AIV studies. However, many other understudied orders have
239 been affected by clade 2.3.4.4 recently [15, 34]. Interaction of different avian orders
240 might contribute to virus dispersal and local persistence [29]. A previous study showed
241 that host origins of HPAIV H5 reassorted genes include Anseriformes, other groups of
242 wild birds, and domestic poultry [25].

243 *Caveats.* A limitation of our results is that the undersampling of viruses in some
244 areas hugely impacted the inferred phylogeography. For example, we cannot conclude
245 if the inferred viral lineage movement from Europe to Qinghai or Japan-Korea occurs
246 directly or if geographically-proximate areas, e.g., central Eurasia, are middle stops of
247 the movement, due to under-sampling in central Eurasia. Despite including sampling
248 size in the phylogeographical analysis, we cannot adjust the geographical sampling biases
249 due to the unknown magnitude of infections at locations. Fortunately, the sampling
250 efforts in some historically under-sampled and no-sampled areas are growing, e.g., in
251 Australia [35]. In the future, given more extensive and evenly-sampled spatial data, our
252 methods could be utilized to understand the role of wild birds in virus dispersal.

253 Despite using empirical bird movement data, our analyses include limited species
254 diversity and dispersal area. Therefore, we did not include the migration volume of
255 birds in the migration network (Figure 1). Currently, bird migration is summarized as a
256 binary network. In the future, integrating comprehensive bird movement models [36, 37]
257 would provide a more detailed understanding of the mechanism of how bird migration
258 contributes to AIV dispersal. Another caveat is that we only considered the HA gene
259 when inferring AIV diffusion and evolution. HA is a key gene in influenza viruses, as
260 it is the receptor-binding and membrane fusion glycoprotein of influenza virus and the
261 target for infectivity-neutralizing antibodies [38]. However, the reassortment events of all
262 internal genes are also important in the dispersal and evolution of HPAIV H5 [25].

263 Our results also show high spatial and temporal heterogeneity in the association
264 strength between specific bird orders and virus lineage movements. Despite the low

265 relative frequency of virus lineage movements during summer breeding and wintering,
266 they may serve as a gene pool for following virus lineage movement during the migration.
267 A previous study emphasizes the important role of the breeding period in interspecies
268 virus transmission in North America [30]. Previous surveillance also shows that LPAI
269 prevalence in waterfowls is higher during the wintering period of Eurasian migratory
270 birds in Africa [39]. Additionally, our results highlight the importance of Suliformes and
271 Ciconiiformes in HPAIV H5 dispersal, which are understudied compared to Anseriformes
272 and Charadriiformes.

273 We did not account for possible interspecies transmission among individuals of mul-
274 tiple bird orders. This is a possible reason for associations between some bird orders
275 and virus dispersal routes where there is no direct bird migration between the origin and
276 destination location. For example, the spring migration of Suliformes and Falconiformes
277 overlaps with virus lineage movements from Japan-Korea to Europe. While birds might
278 not directly fly between the two regions, various species stop between Japan and Europe
279 during migration. Interspecies transmission at the stop-over sites might lead to the virus
280 lineage movements (Figure 2D). However, the under-sampling of the viruses and lack of
281 bird tracking data might also contribute to the observed pattern.

282 Another limitation is that we did not account for variation in movement behaviour
283 within each bird order. Due to limited data, bird order is the most accurate taxonomy
284 level we can study reliably. Finally, we included virus samples from domestic poultry
285 when inferring virus diffusion. Therefore, some patterns in the results could reflect virus
286 transmission between domestic poultry and spillover from wild birds to poultry rather
287 than bird migratory patterns.

288 In conclusion, allocating more resources for global surveillance of avian influenza
289 viruses in wild birds would enhance our ability to tackle the challenges of more viru-
290 lent and transmissible HPAIV H5 spreading in wild birds. To achieve this goal, it is
291 critical to understand “where and in which bird species surveillance is most needed and
292 could have the greatest impact” [17]. Given sufficient data in the future, our framework
293 could help conservation and public health policy-making in designing monitoring and
294 surveillance strategies. More collaboration is needed between ornithologists, movement
295 ecologists, bird conservation experts, avian influenza epidemiologists, disease ecologists
296 and virologists on many aspects, including collaborative data collection/surveillance of
297 AIV and data sharing. For example, if studies were to simultaneously obtain the move-
298 ment tracking of bird populations and their serology and virology surveillance data, then
299 they could link the bird movement directly with the virus transmission and dispersal. In
300 addition, we need more AIV samples from water bodies to better understand environmen-
301 tal transmission. With such data, we would be able to understand the viral transmission

302 at local scales and therefore develop disease models for bird conservation and potential
303 zoonotic threats.

304 4 Materials and Methods

305 4.1 Wild bird movement tracking and distribution modeling

306 To assemble the global wild bird observation data, we accessed the worldwide bird track-
307 ing data from Movebank in 2021. This dataset amassed from 53 studies across the world
308 [40–119]. The Movebank study ID, name, principal investigator, and contact person are
309 listed in Table S6. The dataset is collected by various research groups, and by various
310 sensors, including Global Position System (GPS), Argos, bird ring, radio transmitter,
311 solar geo-locator, and natural mark. It covers over 3542 individual birds (class: Ave),
312 including 10 orders and 95 species (Table S1). For further modelling the migration of the
313 wild birds belonging to different orders, we excluded the observation data on Movebank of
314 Cuculiformes, Caprimulgiformes, Strigiformes, Columbiformes, Phoenicopteriformes, Pi-
315 ciformes, Sphenisciformes, and Procellariiformes, given their paucity and geographically
316 restricted distribution. Additionally, we accessed GPS tracking data of 193 individuals,
317 including 5 orders and 12 Species between 2006 and 2019 in China from a previous study
318 ([120]). Accordingly, we combined the data from China with those on Movebank (Table
319 S6) and finalized a bird observation dataset consisting of 10 orders and 96 species.

320 To model the wild bird distribution throughout a year, we developed a model frame-
321 work based on the species distribution model (SDM). The response variable of the model
322 is bird occurrence (1: presence; 0: pseudo-absence). The independent variables are 20
323 well-studied environmental predictors, including local topography, weather conditions,
324 and time of the season. Table S2 lists the environmental data and the source. We divide
325 the globe into 1-km resolution geographical cells for each month. For each cell, the value
326 of the dependent variable is 1 if there is any observation of an individual in the target
327 order in that month in the bird tracking data, otherwise 0. Furthermore, to infer the
328 probability of bird occurrence between 0 and 1 for each cell, we trained a XGBoost bi-
329 nary classification model [121] for each bird order, respectively. The method is adapted
330 from a previous bird migration model [122]. We used true presence and pseudo-absence
331 data (marked as 1 and 0 respectively). We fitted the distribution of birds which manifest
332 as true-presence data and pseudo-absence data. We randomly divided 67% of the data
333 as the training set and the other 33% as the test set. The model finally outputs the
334 probability of the distribution of migratory birds in each month across years (Dataset 6).
335 The accuracy was evaluated by the area under the curve (AUC) in a test set of the ten

336 orders: Pelecaniformes (0.97), Gruiformes (0.97), Passeriformes (0.97), Suliformes (0.98),
337 Ciconiiformes (0.92), Falconiformes (0.98), Charadriiformes (0.94), Anseriformes (0.90),
338 Accipitriformes (0.90). The modelled wild bird distribution (Dataset 6) was applied in the
339 subsequent analysis to identify key bird orders associated with the global viral dispersal
340 (section 4.3) and local virus emergence.

341 **4.2 Viral sequence data and time-scaled phylogeny of HPAIVs**

342 To infer the phylogeny of avian influenza HPAIV H5 viruses, we accessed sequences of
343 HA genes, NA genes and six internal gene segments from GISAID (Global Initiative on
344 Sharing All Influenza Data [123–125]). Using the sequences, we estimated a maximum
345 likelihood phylogeny (Figure S3) for each gene segment, respectively, under a GTR+ γ
346 nucleotide substitution model, with the randomly selected strains as representatives, by
347 FastTree v2.1.4 [126]. Genotypes of internal gene segments (Figure S3) were defined by
348 clustering pattern with background sequences in a previous study [127]. On the phylogeny,
349 the viruses with internal genes from wild birds, e.g. clade 2.3.2.1 and clade 2.3.4.4, showed
350 wider geographical spread [1, 23], compared to poultry viruses, e.g. clade 2.3.4.1 and clade
351 2.2, despite the high similarity of their HA genes. This demonstrates the importance
352 of gene reassortment in the evolution and transmission of HPAIVs. In this project, we
353 focused on clade 2.3.4.4 and clade 2.3.2.1. Next, we inferred their time-scaled phylogenies
354 of HA genes. Before the inference, to test for the presence of phylogenetic temporal
355 structure, we generated a scatter-plot of root-to-tip genetic divergence against sampling
356 date by TempEst v1.5 [128]. Strong phylogenetic temporal structure was detected in
357 the phylogeny of each clade (Figure S7). The final datasets (Dataset 2) were i) 1163
358 HA sequences of clade 2.3.2.1 ii) 1844 HA sequences of clade 2.3.4.4. The spatial and
359 temporal distribution of the sequences is shown in Figure S4.

360 Time-resolved HA phylogenies were estimated using the Markov chain Monte Carlo
361 (MCMC) approach implemented in BEAST v1.10.4 [129] with the BEAGLE library
362 [130]. We used an uncorrelated lognormal (UCLN) relaxed molecular clock model [131],
363 the SRD06 nucleotide substitution model [132] and the Gaussian Markov random field
364 (GMRF) Bayesian Skyride coalescent tree prior [133]. For each dataset, MCMC chains
365 were run for 300 million (clade 2.3.2.1) and 400 million (clade 2.3.4.4) generations with
366 burn-in of 10%, sampling every 10,000 steps. Convergence of MCMC chains was checked
367 with Tracer v1.7 [134]. A set of 1000 trees for each clade was subsampled from the MCMC
368 chain and used as an empirical tree distribution for the subsequent analysis.

369 **4.3 Discrete trait phylogeography of HPAIVs and counts of** 370 **virus lineage migration**

371 Based on empirical phylogenies, we used a non-reversible discrete-state continuous time
372 Markov chain (CTMC) model and a Bayesian stochastic search variable selection (BSSVS)
373 approach [31] to infer the viral diffusion among locations: i) the most probable locations
374 of the ancestral nodes in the phylogeny and ii) the history and rates of lineage movement
375 among locations [31]. Sampled countries were divided into 10 locations: Africa, Central
376 Asia, Europe, Japan-Korea, North China, South China, Qinghai, Russia, Southeast Asia
377 and USA-Canada. This regional categorization was done according to the major wild bird
378 breeding areas. Furthermore, to estimate the viral gene flows between locations, we used
379 a robust counting approach [135, 136] to count virus lineage migration events. The basic
380 idea is to count the expected number of lineage movements (Markov jumps) between
381 the locations along the phylogeny branches, as applied in previous studies [137–141]. For
382 each location, the frequency distribution throughout a year of the Markov jumps from
383 or to the place is summarized. Using this method, we summarized monthly frequency
384 distribution of the virus lineage migration for each pathway (Figure S5, Dataset 4). This
385 was used for further analysis below.

386 To target the key bird orders for each location, we explored the association of wild
387 bird distribution across a year and the virus diffusion. The monthly wild bird distribution
388 probability at each location (Dataset 5) is generated based on the location's geographical
389 coordinates on the modelled bird distribution probability raster map (Dataset 6). We
390 calculated the correlation between the virus lineage migration and the bird probability
391 distribution at origin and destination regions, respectively, with time lags from -7 to 7.
392 To account for multiple comparisons of 9 bird orders, we use p value $< 0.00556 (= 0.05/9)$
393 to define the statistical significance in the correlations. When bird distribution at the
394 origin leads to the virus lineage movements positively or negatively, we consider the bird
395 order distribution at the origin to be correlated with the virus lineage movements (Table
396 S4.1, Figure 2A). When bird distribution at the sink is positively associated with the
397 virus lineage movement, we consider the bird order distribution at the sink is correlated
398 with the virus lineage movement (Table S4.2, Figure 2A).

399 **4.4 Animal mobility networks and their contribution to HPAIV** 400 **phylogeography**

401 The bird migration network (Figure 1C, D) was summarised by searching publicly avail-
402 able migration data on Movebank. An edge between two locations in the network exists if

403 any migration tracking record shows bird migration. The location-wise live poultry trade
404 values (Dataset 1) were summed up from country-wise import and export of the live
405 poultry recorded on United Nations Comtrade Database (comtrade.un.org/data/). We
406 accessed the total net weight and trade value from 1996 to 2016 of live poultry, including
407 fowls of the species *Gallus domesticus*, ducks, geese, turkeys and guinea fowls. Since
408 there are no accessible data of the within-country poultry trade in China, we adapted
409 the inferred poultry trade accessibility between provinces of China from a previous study
410 [142]. Based on the ratio of the inferred accessibility and the empirical trade value be-
411 tween Hong Kong SAR and the mainland of China, we scaled all the accessibility to the
412 trade value flows among Qinghai, North China and South China.

413 With the summarized seasonal-varying bird migration network, we statistically quan-
414 tified the contribution of wild bird migration to avian influenza virus dispersal. We
415 applied the generalized linear model (GLM) extended Bayesian phylogeography inference
416 [32] with the 1000 empirical trees as the input. The 11 categorized locations in the pre-
417 vious discrete trait phylogeography were still used. The epoch model [33] was used to
418 model the time heterogeneity of the contribution. To explain the contribution of the bird
419 migration and the respective seasonal migration, we also separated the network of spring
420 migration and that of the fall as two predictors for comparison (Figure S6). For each
421 clade and each predictor group, MCMC chains were run for 100 million generations with
422 burn-in of 10%, sampling every 10,000 steps. Similarly, we assessed the convergence of
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902 **6 Figures**

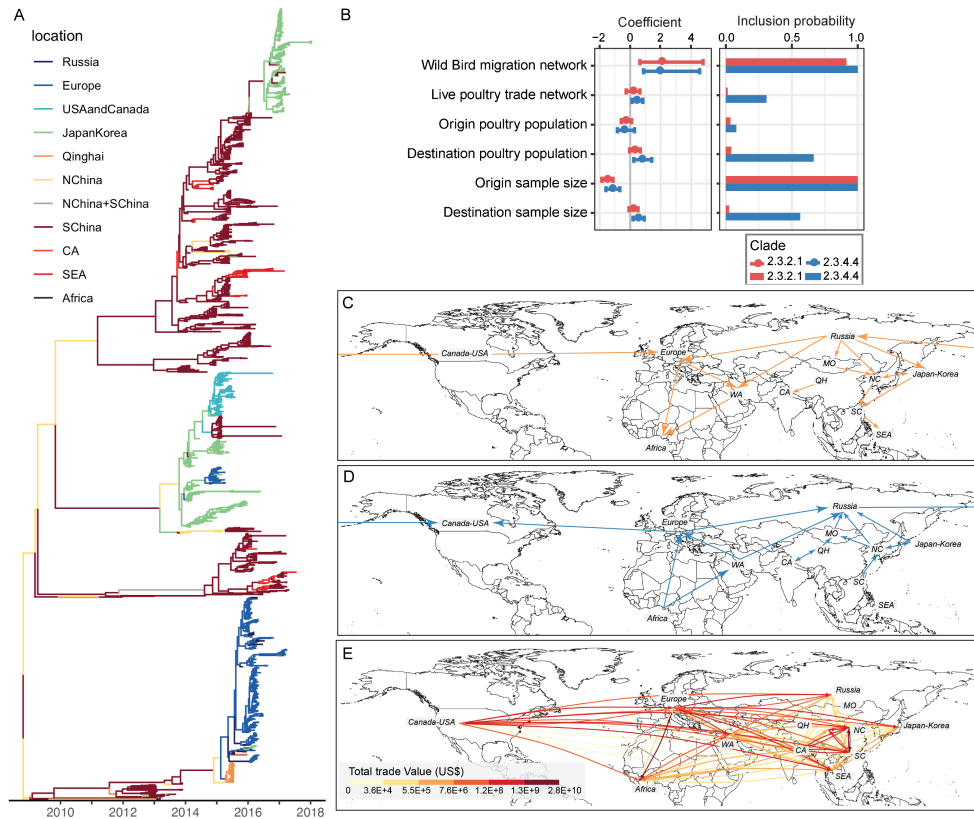


Figure 1: (A) Maximum clade credibility (MCC) time-scaled phylogeny of clade 2.3.4.4 with branches annotated with the inferred location. (B) Contributions of predictors to worldwide diffusion of H5N1 clade 2.3.2.1 and clade 2.3.4.4 inferred from HA genes by GLM-extended Bayesian phylogeographic inference with heterogeneous evolutionary processes through time. Predictors in the model included bird migration network during (C) Northern Hemisphere fall season and (D) Northern Hemisphere spring season, where directed non-weighted edges represent the occurrence of bird migration based on empirical data, and (E) live poultry trade network, where directed weighted edges represent poultry trade value. NChina/NC: North China; SChina/SC: South China; SEA: South-East Asia; CA: Central Asia; QH: Qinghai; MO: Mongolia; WA: Western Asia.

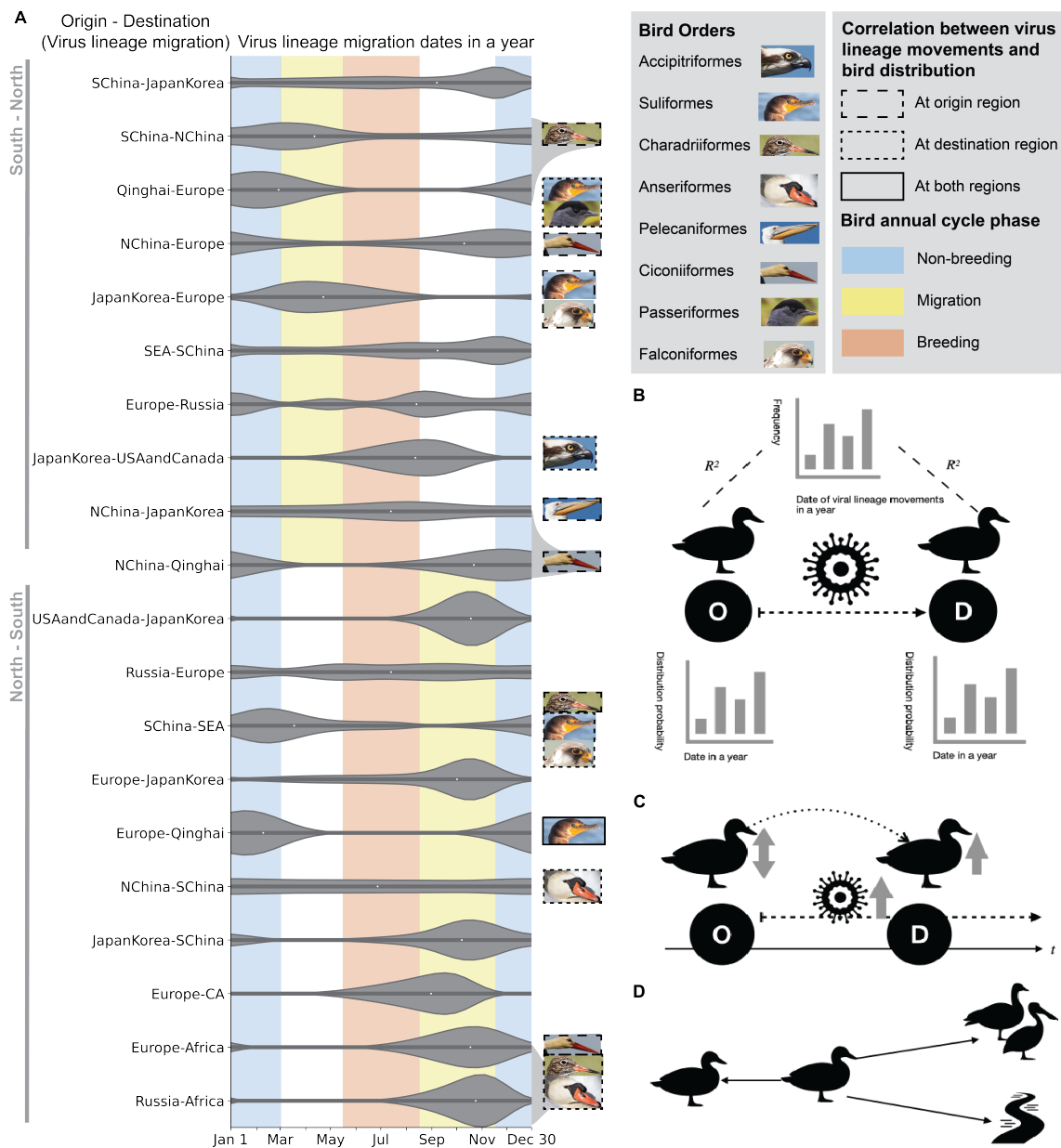


Figure 2: (A) Probability density distribution of the virus lineage migration throughout the year, between locations summarized from the discrete trait phylogeography of HPAIV H5 clade 2.3.4.4 and the Markov jump counts (Section 4.3). X axis: Virus lineage migration dates in a year; labels on Y axis: origin region - destination region of the virus lineage migration. The width of the violins represents the virus lineage migration probability density. Boxes around bird photos show the statistically significant correlation of virus lineage movements and bird order distribution at origin, destination or both regions. Bird species photos were obtained from the Macaulay Library at the Cornell Lab of Ornithology (macaulaylibrary.org). The entries of the photos are listed in Table S5. Non-breeding (blue), migration (yellow) and breeding (red) bird annual cycle phases in general are shown in the south-north migration direction and in the north-south migration direction. (B) Schematic diagram of cross-correlation analyses of virus lineage movement between two locations (O: origin, D: destination) and the bird distribution probability at each location. (C) Time scale of virus lineage movement, bird migration and local virus transmission, including inter-species, inter-individual and environmental transmissions. The grey arrows indicate the increase or decrease of the local bird population and the virus lineage movement influx. (D) Local transmission of AIV includes inter-individual transmission within a population, inter-species transmission within a bird community and potential environmental transmission.

903 **7 Data Availability Statement**

904 We provide Movebank Study ID (unique searchable identifier) and relevant metadata
905 information for Movebank bird tracking data. We also provide accession ID for GI-
906 SAID virus genomic data. All code scripts for analyzing data are provided. All data
907 and scripts are available as a public project <https://doi.org/10.17605/OSF.IO/7A2UK>
908 on Open Science Framework and GitHub Repository <https://github.com/kikiyang/>
909 HPAI_Bird_world.