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2 **Avian influenza spread and seabird movements between colonies**

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5

6 Key-words : spatial disease dynamics, movement ecology, colonial breeding, HPAI H5N1,

7 foraging, migration, prospecting,

8 8 word title, 1206 words, 1 figures, 1 box, Glossary. Teaser of 50 words:

9 **Seabirds have recently been experiencing high rates of mortality across broad scales due**
10 **to Highly Pathogenic Avian Influenza. During breeding, seabird populations are highly**
11 **spatially structured, while over their life, they spend much time at sea. This makes them**
12 **unique systems to document how movement and interspecies interactions affect eco-**
13 **epidemiological dynamics.**

14

15 **Highly Pathogenic Avian Influenza as an additional threat to seabirds**

16 In the current context of global change, threats to seabirds include pressure from invasive
17 species on islands, bycatch, competition with fisheries and climate change impact on food
18 availability [1](Figure 1). Infectious diseases are also becoming increasingly appreciated as a
19 threat as many breeding **colonies** (see Glossary) were recently hit by **Highly Pathogenic**
20 **Avian Influenza (HPAI)** in the North Atlantic Ocean [2]. In the Northern Hemisphere summer
21 of 2022, there was widespread detection of HPAI H5N1 virus in carcasses of dead wild birds

22 and large die offs at seabird colonies [2]. The number of individuals, notably adults, found
23 dead or sick, were very high. For instance, in Scotland, the loss of more than fifty percent of
24 the local population of several of the largest great skua (*Stercorarius skua*) colonies was
25 reported, and several northern gannet (*Morus bassanus*) colonies suffered heavy losses [2].
26 Those outbreaks followed a shift in HPAI epidemiology that started in 2021 and lead to the
27 identification of HPAI as a potential threat to wild birds at broad scale [3]. Some great skuas
28 died of HPAI in 2021 [4] and recurrent HPAI outbreaks in wild birds had been identified, with
29 the possibility that the virus became **enzootic** [5].

30 Waterbirds in general are well-known reservoirs for **Low Pathogenic Avian Influenza (LPAI)**
31 viruses. Work with Anatidae (ducks, geese and swans), shorebirds and gulls [6] on their role
32 in the global circulation of those viruses has contributed to the understanding of the factors
33 affecting avian influenza viral evolution and how the ecological interactions among wild
34 birds along migration flyways promote the maintenance, reassortment, and dispersal of
35 avian influenza viruses [6]. Comparably, little work has been done on pelagic seabirds, which
36 spend a large part of their lives at sea and are seldom affected by HPAI [7].

37 Seabird share life history traits of concern for HPAI interactions: they breed in colonies that
38 are often very dense (Figure 1) where transmission is expected to be high. They spend a
39 large part of their time at sea, where transmission is likely limited (Box 1). Also, as they are
40 long lived, their population dynamics are sensitive to factors affecting adult survival. A
41 critical issue is to identify where direct and environmental faecal-oral transmission of avian
42 influenza viruses occurs within and between species in seabird communities.

43

44 **Mechanism of spread between colonies**

45 How does HPAI spreads between colonies? Seabirds are known for their high breeding site
46 fidelity, so little mixing is expected to happen via **dispersal** (Box 1, Figure I). **Foraging**
47 movements by avian predators and **scavengers**, such as gulls and skuas, are likely involved in
48 the transmission of the virus within a breeding season. A little-noticed outbreak of avian
49 cholera, another infectious bird disease, was described off Newfoundland in 2006-2007:
50 gulls **scavenging** at sea on conspecifics may have been largely responsible for the burst in
51 cases [8]. At an island-scale, Subantarctic skuas (*Stercorarius antarcticus*) have also been
52 identified as potential spreaders of the avian cholera bacterium between local breeding
53 aggregates, with more than 98% of the breeders having antibodies against the disease [9].
54 But in the current pan-northern Atlantic outbreak of HPAI, avian predators and scavengers
55 may only be partly responsible for the spread among breeding populations. Some inter-
56 colony movements have been occasionally documented, notably from birds that are not
57 currently breeding or failed their breeding attempt, however, these movements have been
58 rarely studied. Tracking birds is a massive endeavour done by seabird research teams each
59 season, usually focusing on foraging movements during the breeding season or on winter
60 migration [10]. In most cases, this requires recapturing birds to recover loggers and
61 download data, thus the work is focused on successfully breeding individuals. Some, more
62 costly, loggers enable recovering data remotely, via UHF antennas, GSM or satellite
63 communication. Their use could broaden the scopes of movement studies to include **pre-**
64 **breeders** and **failed breeders**; this could provide key information to assess how infectious
65 agents are transmitted between colonies. Such an approach could provide data on **contact**
66 **structure networks** within and among species to inform models to explore how those could
67 be related to **phylogenetic** data obtained at the same scales.

68

69 **Inferring functional connection among colonies**

70 In addition to the foraging and migratory movements of avian predators and scavengers, the
71 movement of individuals **prospecting** for future breeding sites may be important for the
72 spread of disease agents or parasites [11]. Such movements can occur within a breeding
73 season at a broad range of scales, and often involves failed breeders or pre-breeders [12,13].
74 Given the efforts put by seabird research teams each season for tracking successfully
75 breeding individuals, it may be beneficial to shift some of that focus to the tracking of
76 prospecting individuals to infer functional connection among colonies. Such data would be
77 useful to combine with genetic analyses of the viruses detected on individual hosts, as well
78 as with studies of the spatio-temporal patterns of exposure of birds at colonies and
79 metapopulation dynamics.

80 Earlier work on LPAI in densely breeding and widely distributed seabird species like
81 guillemots *Uria* spp (Figure 1) showed that a high diversity of virus could be detected locally,
82 with evidence of rearrangements of gene segments between locations far apart, stressing
83 the need to explore the ecology and evolution of the interactions at a broad hierarchy of
84 scales [7]. In parallel to phylodynamic studies, sampling of seabird colonies to conduct
85 serological tests should be informative. It could notably allow determining what proportion
86 of individuals were exposed the previous year and how this varies in space and among
87 species, informing us about potential barriers to virus transmission.

88 **Need for integrated approaches**

89 In addition to studying virus evolution, determining contact structure networks within and
90 among species is important for understanding how the risk of transmission is affected by
91 various processes. Evaluating the impact of HPAI on the host individuals and populations is
92 also required. When access to colonies is restricted, drones or field cameras can be used,
93 although detailed data on individuals is often needed. Precise estimates of a key
94 demographic parameters such as the annual survival rates of breeders can be obtained by
95 long-term **capture-mark-recapture** studies. Moreover, capture-mark-recapture studies could
96 be extended to include the monitoring of the exposure of breeding individuals to infectious
97 agents. Surveys conducted on multiple sites are powerful to explore the spatial extent of
98 circulation of infectious agents, while repeated sampling of individuals can provide useful
99 complementary information on local turnover of infection and temporal persistence of
100 immunological status.

101 Such studies may also provide valuable complementary information about the responses of
102 populations to large scale environmental changes, which may involve prospecting followed
103 by dispersal as a key demographic process. In that respect, multisite capture-mark-resighting
104 studies can complement tracking studies using biologing devices, but they require especially
105 strong and coordinated field efforts by teams combining complementary sets of
106 competences.

107 Seabird species, by their highly spatially structured populations during the breeding season
108 and their peculiar ecologies linked to the marine environment, not only represent important
109 communities of species to track the state of the oceans. They also represent unique
110 biological systems to study how demographic, behavioural and epidemiologic processes may

111 interact at hierarchies of scales to explain the responses of metacommunities of hosts
112 threatened by several effects of global change.

113

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144

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150

151 **Figure legend:**

152 **Figure 1: Seabirds aggregate in dense colonies for breeding.** Northern gannets (*Morus*
153 *bassanus*), common guillemots (*Uria aalge*) and great skuas (*Stercorarius skua*) respectively
154 on the islands of Rouzic, France, Hornøya, Norway, and Unst, UK. Massive die-offs related to
155 HPAI H5N1 have been recorded at many seabird colony sites during the 2022 summer in the
156 North Atlantic. Mixed species colonies could represent hotspot of transmission of infectious
157 agents with potential dramatic effects on local and regional populations. Integrative
158 approaches, including movement ecology, are required to decipher the transmission
159 processes at play between and within colonies (pictures © Thierry Boulinier).

160

161

162 **Box 1. Different types of seabird movements that could lead to spread of HPAI strains.**

163 Waterbirds are reservoir host of many LPAI strains, but some HPAI strains, that have evolved
164 under particular circumstances, are very pathogenic for poultry and for some wild species.
165 Migration of waterbirds is important for the global circulation of avian influenza viruses, with
166 evidence of asymmetric flux of viruses along some flyways at continental and
167 intercontinental scales [6]. The dynamics of outbreaks involve shifts in virus ecology
168 associated with changes in opportunities for spread, host susceptibility and pathogenicity,
169 which can be linked to fast evolution of the virus. In particular, recombination among strains
170 can lead to dramatic changes in transmission among hosts. The viruses evolve fast, and
171 studies of their genetic sequences can be used to infer their transmission and the
172 importance of recombination among strains. It is strains of HPAI H5N1 that have been
173 involved in major mortalities of wild and domesticated birds since it emerged in eastern Asia
174 in 1996, but other HPAI exist. gs/GD HPAI H5 is incriminated in the recent seabird die-offs

175 [2,4] and more generally in recent large outbreaks in Europe in poultry and wild birds [5],
176 with the suggestion that it may now be endemic to the area. Given the broad geographic
177 scale and relatively synchronous die-offs due to HPAI H5 detected on seabird colonies in
178 2022, a key issue is to determine what types of seabird movement may have been
179 responsible for the transmission of the virus. Different types of movements of seabirds can
180 be distinguished in relation to their life cycle, each characterized by different geographical
181 scales, timing relative to the breeding season, and potential opportunities for the
182 transmission of infectious disease agents between individuals of the same or different
183 species (Figure I)[11]. Birds foraging at sea, while in flight or on the water, have been
184 suggested to be unlikely to transmit infectious agents between each other [11], although
185 particular types of behaviours warrant consideration in the case of highly transmissible
186 agents that can survive in the marine environment such as HPAI H5N1: feeding aggregations
187 behind fishing boats or on shoals of fish, dense rafts on the water, predation or
188 **kleptoparasitism** (Figure II, A and B).

189 **Figure I: Illustrations of the different types of movements of seabirds and opportunities for**
190 **virus transmission.** Transmission could occur while foraging at sea, winter migration or
191 prospecting between colonies (printed from Boulinier *et al.* 2016 [11] by permission of
192 Oxford University Press).

193 **Figure II: Example of at-sea interactions.** (A) and (B) great skuas (*Stercorarius skua*)
194 harassing northern gannets (*Morus bassanus*) to obtain food by kleptoparasitism (pictures ©
195 Thierry Boulinier).

196

197 **Glossary**

198 **Capture-mark-recapture:** The capture, marking and recapture or resighting of individuals is
199 used to estimate demographic parameters and conduct behavioural studies. Samples for
200 disease investigations can be collected when an individual is captured, such as blood sample
201 for detecting antibodies as a sign of past exposure to an infectious agent, or swabs for direct
202 detection of the agent. Longitudinal data acquired within such a framework can be very
203 informative, especially in long lived species like seabirds.

204 **Colonies:** aggregates of breeding territories.

205 **Contact structure networks:** for directly or environmentally transmitted infectious agents
206 such as avian influenza viruses, identifying the network of spatio-temporal association and
207 contacts between individuals is important to infer transmission risks.

208 **Detectability:** the probability of observing an event that occurred. Detectability is often
209 lower than one in wildlife population or disease ecology studies. Particular sampling designs
210 and statistical modelling are available to estimate parameters in such cases, notably when
211 capture-mark-recapture data are available.

212 **Dispersal:** an ecological process that involves the movement of an individual or multiple
213 individuals away from the population in which they were born or reproduced to another
214 location, or population, where they will settle and reproduce.

215 **Enzootic:** an infectious agent is enzootic in a population when the infection is maintained in
216 the population without the need for external inputs.

217 **Failed breeder:** individual that attempted breeding the current year, but failed its attempt,
218 either before laying an egg, after laying an egg, or after its eggs hatched.

219 **Foraging:** behaviour associated with the search of food.

220 **HPAI:** Highly Pathogenic Avian Influenza. HPAI viruses can recombine with LPAI, which can
221 change their properties and can be responsible for increase in transmission or pathogenicity.

222 **Kleptoparasitism:** a form of feeding in which one animal deliberately takes food from
223 another. This might be an opportunity for the transmission of highly transmissible infectious
224 agents.

225 **LPAI:** Lowly Pathogenic Avian Influenza. Waterbirds are reservoirs of a broad set of LPAI
226 viruses. LPAI viruses can recombine with HPAI, which can change their properties and can be
227 responsible for increase in transmission or pathogenicity.

228 **Phylodynamic:** phylodynamic approaches combine evolutionary, demographic and
229 epidemiological concepts to track genetic changes.

230 **Pre-breeder:** an individual that has not bred yet, but which may attend breeding areas.
231 Seabirds are long lived and in most species first breeding is delayed until several years after
232 hatching and pre-breeders start to visit colonies the years before.

233 **Prospecting:** visit of a breeding area by an individual that does not currently breed there.

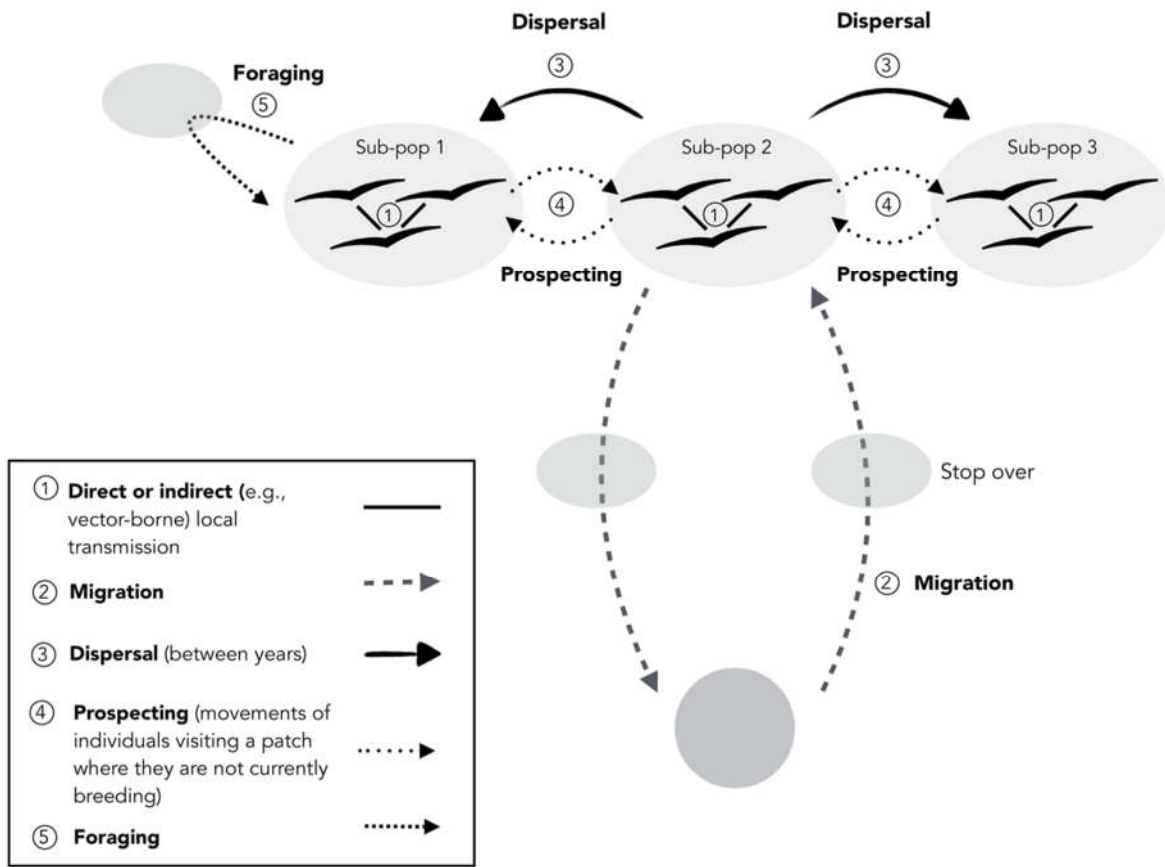
234 **Scavenging:** Scavengers are animals that consume dead organisms that have died from
235 causes other than predation or have been killed by other predators. Scavenging is an
236 opportunity for the transmission of infectious agents.

237



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