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Avian influenza spread and seabird movements between colonies

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

Highly Pathogenic Avian Influenza as an additional threat to seabirds

In the current context of global change, threats to seabirds include pressure from invasive species on islands, bycatch, competition with fisheries and climate change impact on food availability [1](Figure 1). Infectious diseases are also becoming increasingly appreciated as a threat as many breeding **colonies** (see Glossary) were recently hit by **Highly Pathogenic Avian Influenza** (**HPAI**) in the North Atlantic Ocean [2]. In the Northern Hemisphere summer of 2022, there was widespread detection of HPAI H5N1 virus in carcasses of dead wild birds and large die offs at seabird colonies [2]. The number of individuals, notably adults, found dead or sick, were very high. For instance, in Scotland, the loss of more than fifty percent of the local population of several of the largest great skua (*Stercorarius skua*) colonies was reported, and several northern gannet (*Morus bassanus*) colonies suffered heavy losses [2]. Those outbreaks followed a shift in HPAI epidemiology that started in 2021 and lead to the identification of HPAI as a potential threat to wild birds at broad scale [3]. Some great skuas died of HPAI in 2021 [4] and recurrent HPAI outbreaks in wild birds had been identified, with the possibility that the virus became **enzootic** [5].

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

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

Mechanism of spread between colonies

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

Inferring functional connection among colonies

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

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

Need for integrated approaches

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

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

Seabird species, by their highly spatially structured populations during the breeding season and their peculiar ecologies linked to the marine environment, not only represent important communities of species to track the state of the oceans. They also represent unique biological systems to study how demographic, behavioural and epidemiologic processes may interact at hierarchies of scales to explain the responses of metacommunities of hosts threatened by several effects of global change.

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Figure legend:

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

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

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

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

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

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

Glossary

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

Colonies: aggregates of breeding territories.

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

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

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

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

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

Foraging: behaviour associated with the search of food.

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

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

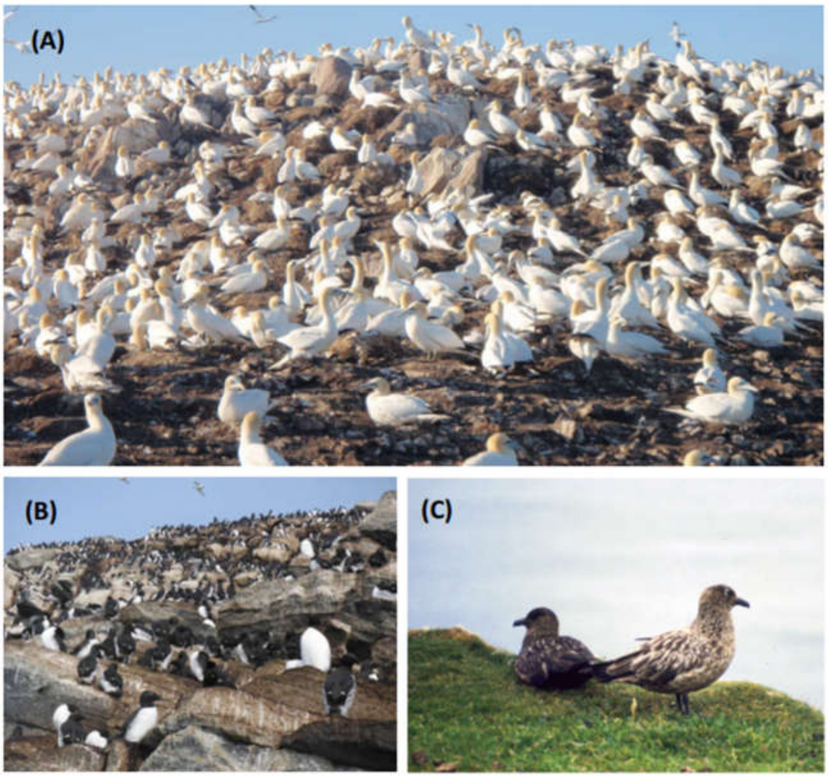
LPAI: Lowly Pathogenic Avian Influenza. Waterbirds are reservoirs of a broad set of LPAI viruses. LPAI viruses can recombine with HPAI, which can change their properties and can be responsible for increase in transmission or pathogenicity.

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

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

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

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


(A)
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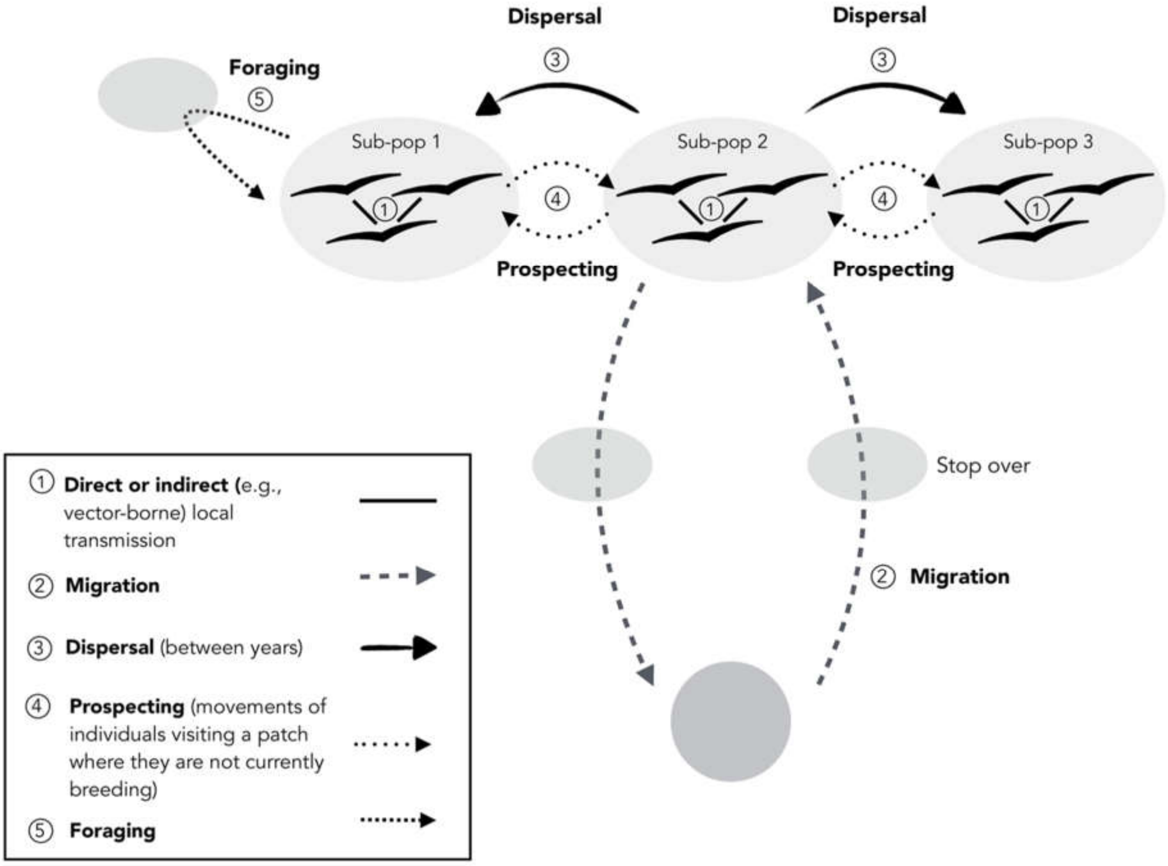
Dispersal
③
Dispersal
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Foraging
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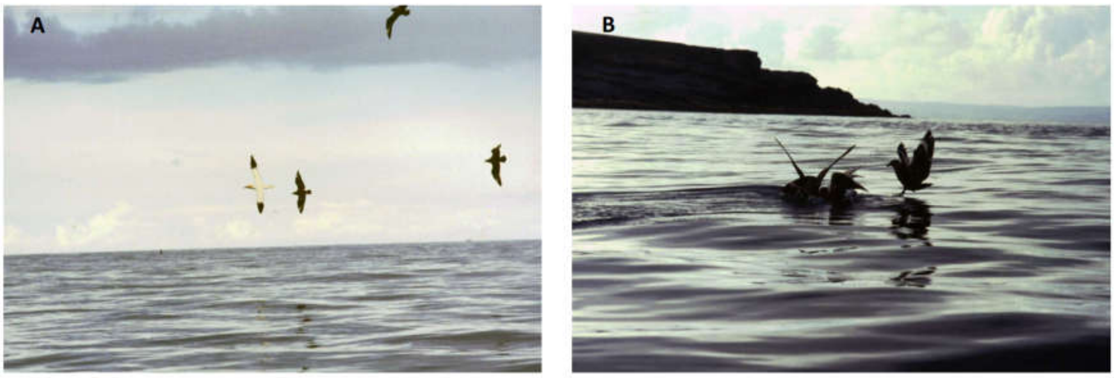
Sub-pop 1
Sub-pop 2
Sub-pop 3
①
①
①
④
④
Prospecting
Prospecting
Stop over
② Migration
① Direct or indirect (e.g., vector-borne) local transmission
② Migration
③ Dispersal (between years)
④ Prospecting (movements of individuals visiting a patch where they are not currently breeding)
⑤ Foraging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