

1 **Strong breeding colony fidelity in northern gannets following High Pathogenicity Avian
2 Influenza Virus (HPAIV) outbreak**

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4 David Grémillet^{1,2}, Aurore Ponchon^{3,4}, Pascal Provost⁵, Amandine Gamble^{6,7}, Mouna Abed-
5 Zahar⁸, Alice Bernard¹, Nicolas Courbin¹, Grégoire Delavaud⁵, Armel Deniau⁵, Jérôme Fort⁹,
6 Keith C. Hamer¹⁰, Ruth Jeavons¹⁰, Jude V. Lane¹¹, Liam Langley¹², Jason Matthiopoulos⁶,
7 Timothée Poupart¹³, Aurélien Prudor¹, Nia Stephens¹⁴, Alice Trevail¹², Sarah Wanless¹⁵,
8 Stephen C. Votier¹⁶ and Jana W.E. Jeglinski⁶

9

10 ¹ CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

11 ²FitzPatrick Institute, DST/NRF Excellence Centre at the University of Cape Town, Rondebosch 7701, South Africa

12 ³ School of Biological Sciences, University of Aberdeen, Scotland, UK

13 ⁴ IMBE, Aix Marseille Univ., Avignon Univ., CNRS, IRD, Marseille, France

14 ⁵ Ligue pour la Protection des Oiseaux, Réserve Naturelle Nationale des Sept-Îles, Pleumeur Bodou, France

15 ⁶School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Scotland, UK

16 ⁷ Department of Public and Ecosystem Health, Cornell University, New York, United States

17 ⁸ LABOCEA, 2 rue du sabot, 22440 Ploufragan, France

18 ⁹ Littoral, Environnement et Sociétés, LIENSs, UMR 7266 CNRS-La Rochelle University; La Rochelle, France

19 ¹⁰ School of Biology, University of Leeds, UK

20 ¹¹ RSPB Centre for Conservation Science, Cambridge, UK

21 ¹² Centre for Ecology and Conservation, University of Exeter, Penryn, Cornwall, UK

22 ¹³ PatriNat, OFB-CNRS-MNHN, Muséum national d'Histoire naturelle, Paris, France

23 ¹⁴ RSPB Ramsey Island, St Davids, Pembrokeshire UK

24 ¹⁵ UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Scotland, UK

25 ¹⁶ Lyell Centre, Institute for Life and Earth Sciences, Heriot-Watt University, Edinburgh, UK

26 Abstract:

27 High pathogenicity avian influenza virus (HPAIV) caused the worst seabird mass-mortalities
28 on record in Europe across 2021-2022. The northern gannet (*Morus bassanus*) was one of the
29 most affected species, with tens of thousands of casualties in the northeast Atlantic between
30 April-September 2022. Disease outbreaks can drastically modify the movement ecology of
31 animals and diminish spatial consistency, thereby increasing the potential for disease
32 transmission. To detect potential changes in movement behaviour, we GPS-tracked breeding
33 adults following the initial HPAIV outbreak, at three of the largest gannet breeding colonies
34 where major mortality of adults and chicks occurred (Bass Rock, Scotland, UK; Grassholm,
35 Wales, UK; Rouzic island, Brittany, France). Crucially, GPS-tracked birds remained faithful to
36 their breeding sites and did not prospect other breeding colonies. They performed regular
37 foraging trips at sea, similar to their behaviour before the outbreak. Gannet foraging effort
38 was nonetheless lower than in 2019, thus surviving birds may have benefited from reduced
39 intra- and interspecific food competition. Breeding colony fidelity of adult northern gannets
40 following HPAIV mass-mortalities suggests limited long-term capacity to virus spread, which
41 may contrast with the behaviour of adults during the disease outbreak, or with that of
42 younger individuals.

43

44 Keywords: Avian pathogens, Behavioural latency, Density-dependence, Movement ecology,
45 Seabird conservation, Viral transmission

46

47 **Introduction**

48 Avian influenza was first reported in farmed poultry in 1878 in Northern Italy (Perroncito,
49 1878). Outbreaks of the virus occurred worldwide in domestic fowl across the 20th century
50 (Swayne and Suarez, 2000). During this period, wild birds were also regularly affected
51 (Gauthier-Clerc et al., 2007). In 1996, a form of highly pathogenic avian influenza virus
52 (HPAIV; H5Nx clade 2.3.4.4) evolved in farmed poultry in Southern China. It subsequently
53 spilled over to wild birds, and occasionally to humans (Alexander and Brown, 2009). HPAIV
54 has since occurred in 61 countries and is endemic in poultry farms around the world. In
55 2021/2022, the worst-ever HPAIV outbreak was recorded in poultry farms, especially in
56 Europe (Wille and Barr, 2022), resulting in the culling of an estimated 47.7 million birds
57 (Authority et al., 2022). These events deeply challenge intensive bird farming, as high-density
58 housing conditions and long-distance poultry transport lead to the spread of HPAIV, and to
59 the suffering and slaughter of captive animals (Kuiken and Cromie, 2022). Rapid evolution in
60 high-density, confined poultry farms also enhances the likelihood of mutations leading to the
61 emergence of HPAIV as the next human pandemic (Roberts Jr and Krilov, 2022). Finally, HPAIV
62 is now causing substantial mortalities to wild birds, including in species already challenged by
63 other human activities (Gamarra-Toledo et al., 2023).

64 This is the case for seabirds, which stand out as the most endangered bird group beyond
65 parrots (Dias et al., 2019). Half of the worldwide abundance of seabirds has been lost since
66 1970 (Grémillet et al., 2018), mainly because of breeding habitat loss, mortality caused by
67 fishing gear, invasive species (e.g. cats and rats), food competition with fisheries, direct and
68 indirect consequences of climate change, and pollution (Dias et al., 2019; Grémillet et al.,
69 2018). Pathogens can also have significant impacts on seabird populations, as demonstrated
70 by avian cholera (*Pasteurella multocida*) affecting Cape cormorants (*Phalacrocorax capensis*)
71 in South Africa (Crawford et al., 1992), or common eiders (*Somateria mollissima*) in North
72 America (Iverson et al., 2016). While seabirds are common hosts of low pathogenicity avian
73 influenza viruses (LPAIV) (Lang et al., 2016), HPAIV has rarely been detected in this group
74 before the 2021-2022 outbreak, except in Southern Africa where recurrent HPAIV outbreaks
75 have affected seabirds since 2016 (Molini et al., 2020). Now, for the first time, HPAIV is
76 significantly affecting European seabird populations, with the virus spreading to e.g. 12
77 species in the UK (Falchieri et al., 2022). With tens of thousands of casualties in 2022 in the

78 Northeast Atlantic, northern gannets (*Morus bassanus*) are among the most affected species,
79 together with great skuas (*Stercorarius skua*) and sandwich terns (*Thalasseus sandvicensis*).
80 Gannets are an iconic species that attract conservation and media interest, in their own right,
81 but also as umbrella species for the marine environment. Despite living in some of the most
82 anthropogenically modified marine regions of the planet (e.g. the North Sea), gannet
83 populations consistently increased across their distribution zone in the northeast Atlantic
84 during the second half of the 20th century (Grandgeorge et al., 2008) - until the 2022 HPAIV
85 outbreak.

86 The present HPAIV panzootic highlights the urgent need for a better understanding of the
87 impact of such disease outbreaks on the movement ecology of affected species, both during
88 and following HPAIV outbreaks, and the associated consequences for disease transmission.
89 Seabirds such as gannets are organised as metapopulations where colonies are connected
90 through dispersal movements of pre-breeding birds (Jeglinski et al., 2022). In contrast,
91 breeding seabirds generally show very high fidelity to their colony and to their breeding site
92 (Hamer et al., 2001). As central place foragers, they travel large distances away from their
93 breeding colony to their foraging sites at sea, but many species show a marked degree of
94 repeatability in their individual movement and space use patterns (Guiry et al., 2022).
95 Gannets in particular have also been shown to forage in colony-specific non-overlapping areas
96 (Wakefield et al., 2013) suggesting a limited capacity for close contact (and thus potential
97 transmission routes) between breeders from different colonies. However, it is currently
98 unclear how disease and the disruption caused by a disease outbreak affect the predictable
99 movement patterns of seabirds, both in the short-term (i.e. during a disease outbreak) or in
100 the long-term (i.e. following a disease outbreak).

101 Bird aggregations, especially dense seabird colonies, function as information centres (Evans
102 et al., 2016) where birds glean public information from their conspecifics, such as the location
103 of potential food resources at sea (Courbin et al., 2020), or the quality of local breeding
104 habitats (Danchin et al., 1998). During the 2022 HPAIV outbreak, when many chicks and adult
105 gannets died at breeding colonies, surviving adult gannets were exposed to public
106 information signalling that they were breeding in a highly hazardous habitat. As a short-term
107 effect of such disturbance, we might expect to see drastic changes in movement and space
108 use patterns. Indeed, recent work has demonstrated that adults black-legged kittiwakes

109 (*Rissa tridactyla*) that perceived their breeding habitat as poor immediately modified their
110 movement patterns (Ponchon et al., 2017): Adults which failed breeding thereby switched
111 from exclusively commuting between their nest and foraging areas at sea, to visiting other
112 breeding colonies to prospect for better nesting spots. Prospecting behaviour was also
113 recorded in 12 out of 14 gull and tern species studied in Europe and North America, even
114 when individuals were successfully breeding (Kralj et al., 2023). Such changes in movement
115 patterns increase the potential for disease transmission, by increasing the likelihood of
116 contact, be it on land or at sea, between birds from different colonies (Boulinier, 2023;
117 Boulinier et al., 2016).

118 Further, we do not know whether a disease outbreak has longer lasting effects on movement
119 and space use of surviving animals. For example, seabird mass-mortalities are likely to reduce
120 food competition for surviving individuals and may therefore lead to modified foraging
121 patterns. Short-term effects on movement, such as the increase in prospecting frequency
122 described above, could become a more permanent feature. This would lead to increased
123 connectivity between usually segregated breeding colonies and thus have the potential to
124 maintain enhanced disease transmission, within gannet metapopulations and at the scale of
125 multispecies seabird communities (Boulinier et al., 2016). Finally, survivors could make
126 permanent decisions regarding their terrestrial space-use by abandoning their breeding
127 colony, as shown in Cape cormorants or Double-crested cormorants (*Phalacrocorax auritus*)
128 which desert breeding colonies entirely when exposed to avian cholera or Newcastle disease
129 virus (Crawford et al., 1992; Leighton et al., 2021). It is uncertain whether gannets display
130 such short or long-term behavioural shifts, because they are known for their high fidelity to
131 nesting (Nelson, 1966), and foraging sites (Votier et al., 2017; Wakefield et al., 2015). Also,
132 studies on closely-related cape gannets (*Morus capensis*) showed that, even when confronted
133 with strongly degraded environmental conditions and ecological traps, adult breeders kept
134 the same breeding and foraging locations (Grémillet et al., 2016; Pichegru et al., 2010).

135 Previous investigations have described the movement ecology of seabirds, e.g. Indian yellow-
136 nosed albatrosses (*Thalassarche carteri*) (Ponchon et al., 2021) or brown skuas (*Stercorarius*
137 *antarcticus*)(Lamb et al., 2022) exposed to avian cholera. Yet, to the best of our knowledge,
138 no study has investigated seabird movements following an HPAIV outbreak, and very few did
139 so in other birds (Gaidet et al., 2010). We used the rare opportunity to fill this critical gap in

140 three of the largest gannet breeding colonies in the Northeast Atlantic which experienced
141 very high levels of HPAIV-related chick and adult mortality; the Bass Rock in Scotland (UK),
142 Grassholm in Wales (UK), and Rouzic Island in Brittany (France). Bass Rock was, before the
143 HPAIV outbreak, the largest northern gannet colony in the world, with an estimated 75,259
144 breeding pairs (Murray et al., 2014). Taken together, the three studied colonies totalled ca.
145 26% of the northern gannet world population (134,259 out of 525,694 pairs (Murray et al.,
146 2015)).

147 We focussed on the longer-term effect of the HPAIV outbreak on breeding gannet space use,
148 since potential persistent behavioural shifts may maintain a high degree of transmission
149 potential in the metapopulation (Boulinier, 2023). We also provide some background
150 epidemiological information and data on gannet colony dynamics during the outbreak. The
151 outcome of our study has strong implications for understanding the potential of breeding
152 gannets as vectors of HPAIV.

153

154 Methods

155 Northern gannets were studied in May-October 2022 on Bass Rock, Scotland (56°04'N,
156 2°29'E), Grassholm, Wales (51°43'N, 05°28'W), and Rouzic Island, Brittany (48°54'N, 3°26'W).
157 All personnel involved in field operations were equipped with full-body suits and disposable
158 gloves, face masks, goggles and caps. Biocides (Virkon® or SafeFour®) were used between
159 each manipulated bird to clean clothing, shoes and equipment.

160

161 Characterization of the HPAIV outbreak:

162 - Bass Rock:

163 On 4th June 2022, unusual numbers of dead and dying gannets were observed on Bass Rock
164 (Scottish Seabird Centre, pers. comm., see also Suppl. 1). Due to permit issues, gannets
165 equipped with GPS-GSM tags (see below) were not screened for HPAIV.

166 - Grassholm:

167 Following an unusually high number of dead gannets at the colony, HPAIV was confirmed
168 from Grassholm on 3rd August with no further access to site permitted for the rest of the
169 breeding season.

170 - Rouzic:

171 Mortality affecting adult gannets was first recorded on 1st July 2022 on the live camera
172 monitoring the Rouzic colony. Samples were subsequently collected from 31 live or dead
173 gannets in, and around the Rouzic colony between July and September 2022, for HPAIV
174 screening and characterization. We thereby performed opportunistic necropsies on four adult
175 birds found dead on the colony, from which we collected tracheal and cloacal swabs and/or
176 lung and trachea samples. We also collected cloacal swabs, tracheal swabs and/or external
177 wipes impregnated with sterile distilled water (applied to the feathers and featherless areas
178 of the birds) from live individuals showing no HPAIV symptoms, including 15 adult birds
179 equipped with GPS-GSM loggers (see below), and 12 recently fledged juvenile birds captured
180 at sea or in the colony. We also collected plasma samples from seven of these juvenile birds.
181 All samples were stored at -20°C until laboratory analyses.

182 Samples were analysed using the protocols recommended by the French Ministry of
183 Agriculture and based on the recommendations provided by the OIE/FAO international
184 reference laboratory for avian influenza. Tissue and swab samples were screened for HPAIV
185 genetic material by real-time reverse transcription polymerase chain reaction (rRT-PCR)
186 targeting the M gene. To identify the subtype of the circulating virus, positive samples were
187 then typed using an rRT-PCR targeting either the H5 or H7 type of the haemagglutinin gene.
188 One sample testing positive for H5 was analysed for further characterization of the virus with
189 an RT-PCR discriminating HP H5 of the 2.3.4.4b clade, and an RT-PCR targeting the N1 type of
190 the neuraminidase gene. Samples testing negative for host genetic material were classified as
191 inconclusive, likely due to the degradation of the samples, and were excluded from the study.
192 Plasma samples were screened for antibodies specifically targeting H5N1, H5N3, H5N5 or
193 H5N8 by haemagglutination inhibition (HI). Collected samples and associated laboratory
194 results are summarized in Table S2 (Suppl. 2).

195

196 GPS tracking:

197 To study their movement ecology following the initial HPAIV outbreak, we deployed GPS-GSM
198 tags on breeding adult gannets with chicks which showed no HPAIV symptoms on the Bass
199 Rock (11th to 13th August 2022) and on Rouzic (23rd to 26th August 2022), about two months
200 after the first signs of the disease were noticed in both colonies. GPS-GSM tags are pre-
201 programmed to send data to a server using the 2G mobile-phone network so that data can
202 be transmitted from anywhere within 2G coverage and accessed by the user in near-real-
203 time. At Grassholm, birds were fitted with remotely-downloadable tags that send data via a
204 UHF link to a base station deployed at the breeding colony in May 2022. At this location five
205 tags were still operational 18th August to 19th September 2022.

206 For these GPS deployments, adults rearing chicks (2 to 8 weeks old) were caught at the nest
207 and handled so as to minimize stress: the procedure lasted < 10 min and birds were kept in
208 the shade. Tags were attached with Tesa® tape to the three central tail feathers. For Bass
209 Rock gannets, we used nanofix tags (Pathtrack Ltd., solar powered, mass 18 g, 0.7% of bird
210 body mass, dimensions 56x28x15mm plus ~40 mm external whip antenna). These tags
211 recorded one GPS position each 15 min or 30 min, depending on battery voltage. For
212 Grassholm gannets, we used axy-trek remote tags (Technosmart solar powered, mass 15 g, <
213 0.5% of bird body mass, dimensions 52x25x15 mm). For Rouzic gannets, we used OrniTrack-
214 9 tags (Ornitela, solar powered, mass 9 g, 0.3% of bird body mass, dimensions 37x19x12 mm,
215 plus ~10 cm external whip antenna). These tags were programmed to record a GPS position
216 each 60 min at night, and each 15 min, 30 min or 60 min during the day, depending on battery
217 voltage. We planned for tags to fall off once birds were starting to moult their tail feathers -
218 previous deployments lasted up to 3 - 5 months (J. Jeglinski, D. Grémillet, unpublished data).
219 At all three colonies we weighed gannets to the nearest 10 g. All birds were ringed with a
220 metal ring and plastic ring with a unique alphanumeric combination. Once released, most
221 birds returned immediately to their nests. We monitored chicks after capture until the
222 captured parent had returned, generally immediately, at the latest within 1 h after capture.

223 GPS Data processing:

224 Data were analyzed using R version 4.1.2 (R Core Team 2021). Data from Rouzic, which are
225 stored in the Movebank database, were imported with the *move* R package (Kranstauber et
226 al., 2022) while data from Bass Rock and Grassholm were imported from csv files.

227 For the three datasets, at-sea trips were discriminated from periods in the colony when the
228 birds were > 1 km away from the colony for > 1 h. Trips with time gaps longer than 10 h and
229 incomplete trips were excluded, which represented 13.9% of trips for Bass Rock, 27.3% for
230 Grassholm and 18.4% for Rouzic. At-sea locations were linearly interpolated with a 15min
231 time resolution using the *pastecs* package (Grosjean et al., 2018). Two consecutive locations
232 (= 30 min) in any other gannet colony were considered as prospecting.

233 We calculated trip characteristics (maximal distance to the colony in km, total trip duration in
234 hrs and total distance travelled in km) as well as the time spent in the colony between at-sea
235 trips in hrs, and present these averaged for each individual and then averaged by colony in
236 Table 1. We fitted linear mixed models separately for each colony dataset using the respective
237 trip characteristics for each bird as response variables to test whether log-transformed trip
238 characteristics and time spent in the colony between at-sea trips changed significantly over
239 time (converted as day since 10th August 2022, first day of the study period). Bird ID was
240 included as a random effect.

241 Inferring at-sea behavioural states:

242 A 3-state hidden Markov model (HMM) was fitted to the at-sea interpolated location dataset
243 from all three colonies combined, using the *moveHMM* package (Michelot et al., 2016). The
244 states can be interpreted to reflect three different activities at sea: (1) resting, characterised
245 by a small step length and low turning angle, (2) travelling, characterised by a long step length
246 and low turning angle and (3) foraging, characterised by an intermediate step length and a
247 large turning angle. A set of different initial parameter values was used to ensure that the
248 global maximum log-likelihood had been reached. The Viterbi algorithm was used to classify
249 the most likely behaviour at each location and proportions of each activity occurring during
250 one at-sea trip were calculated, averaged by individual and then, by colony. We fitted logistic
251 regressions to the proportions of each activity during a trip for each bird as response variables
252 using the *glmmTMB* package (Brooks et al., 2017), accounting for zero-inflated data, to test

253 whether activity proportions changed over time (converted as day since 10th August 2022,
254 first day of the study period). Bird ID was included as a random effect.

255

256 Results:

257 Gannet colony dynamics:

258 The impact of HPAIV on the Bass Rock was extremely high, with thousands of dead gannets
259 in the colony and washing up on the surrounding beaches. A drone survey on 30th June 2022
260 counted 21,277 gannets (Lane et al. unpubl. data), whereas a previous census counted 75,259
261 apparently occupied sites (AOS) in 2014 [38]. The two counts use slightly different metrics,
262 but they suggest at least 71% decline in AOS during the 2022 HPAIV outbreak. Direct
263 observations on Bass Rock also indicated that at least 75% of active nests disappeared during
264 the 2022 breeding season (Lane et al. unpubl. data). On Grassholm, adult and chick mortality
265 were extremely high with many thousands of birds dead on the colony and in the surrounding
266 waters. On Rouzic, aerial pictures of the colony revealed that AOS numbers declined from
267 18,839 on 17/05/2022, to 8,625 on 28/08/2022 (54% decline during the breeding season).
268 Observations via the live camera installed on the breeding colony estimated that >90% of
269 chicks died during the same period (Suppl. 1). More detailed, weekly counts performed
270 between 11/07/2022 and 30/09/2022 on five sections of the colony containing 40-102 AOS,
271 suggested that between 58-87% of breeding adults died, and between 67-94% of the chicks
272 (see Suppl. 3).

273

274 Characterization of the HPAIV outbreak

275 - Bass Rock:

276 Analysis of samples from dead gannets by the Animal and Plant Health Agency (APHA), UK,
277 confirmed an outbreak of HPAIV H5N1 (Scottish Seabird Centre, pers. comm.).

278 - Grassholm:

279 Following unusual gannet mortality in late July, four birds from 21st July were confirmed as
280 positive for HPAIV H5N1 by APHA.

281 - Rouzic island:

282 The first necropsy samples collected from a dead adult found on the colony on 11th July 2022
283 tested positive for HPAIV. Laboratory analyses conducted on samples collected from a bird
284 found dead on the colony on 30th September 2022 confirmed the circulation of HPAIV H5N1
285 clade 2.3.4.4b in the colony. HPAIV H5 was also detected in live birds: 1/9 cloacal swabs from
286 adults subsequently equipped with GPS, and 2/7 external wipes from juveniles (recently
287 fledged and captured on land/at sea) tested positive for HPAIV H5. All the cloacal and tracheal
288 swabs collected from these juveniles, as well as from 5 other juveniles were classified as
289 negative or inconclusive, suggesting varying detection probabilities across sample types (see
290 Suppl. 2). Antibodies against H5N1 were detected in 4/7 juveniles (including the 2 with RT-
291 PCR-positive external swipes). These individuals also tested positive for antibodies against
292 H5N5 and H5N8, and to a lesser degree, for antibodies against H5N3, although higher titers
293 were systematically observed for H5N1 (Suppl. 2), suggesting cross-reactions with other
294 serotypes. None of the samples tested positive for HPAIV H7.

295

296 Movement ecology:

297 All 10 GPS tags deployed on Bass Rock gannets sent GPS positions. On Grassholm, 5 out of 11
298 deployed tags provided data during the study period. For Rouzic, 13 out of 15 tagged
299 individuals remained in the English Channel. One gannet, sampled at tag deployment, tested
300 positive to HPAIV and never provided GPS positions, and another (tested negative at tag
301 deployment) initiated migration after being equipped, moving toward West Africa without
302 touching land until the tag stopped sending data on 16th November 2022. (Table 1). Average
303 gannet body mass was 3230±298g (Bass Rock), 3004±325g (Grassholm), and 2920±240g
304 (Rouzic), which is in line with breeding gannet body mass in previous years (Le Bot et al.,
305 2019).

306 While alive, none of the gannets came ashore anywhere outside of their respective breeding
307 colonies during the GPS data transmission period. Overall, gannets from Bass Rock, Grassholm
308 and Rouzic did not change their space use across the 4-8 weeks study period and foraged
309 consistently in the same areas (Fig. 1). Birds from Rouzic did not change their at-sea trip
310 characteristics over time (similar duration, maximal distance to the colony and total distance

311 travelled; Table 2; Fig. 2a-c), but they slightly decreased the time spent at the colony between
312 at-sea trips (Table 2; Fig. 2d). Among them, one individual was found dead on a beach on the
313 island of Guernsey (82 km Northeast of Rouzic), 14 days after being equipped. This individual
314 was not tested for HPAIV when found dead, and its behaviour for the time period during
315 which we received GPS data did not differ from that of other Rouzic birds we tracked. Birds
316 nesting on Bass Rock spent the same amount of time attending their colony but increased the
317 duration of their at-sea trips marginally, travelling slightly further and longer in distance and
318 time (Table 2; Fig. 2). Birds from Grassholm did not change any trip characteristics nor their
319 nest attendance patterns. Considering their activity budgets during trips, birds maintained
320 the same proportions of time spent foraging, flying and resting on the water, regardless of
321 their colony (Table 2; Fig. 3). For the 3 colonies, compared to early chick-rearing in 2019, at-
322 sea trips were 47-58% shorter in maximal distance and total distance travelled and 10-53%
323 shorter in duration (Suppl. 4).

324

325 **Table 1.** Sample size, foraging trip characteristics, percentage of activities and colony
326 attendance of northern gannets nesting on Rouzic, Grassholm and Bass Rock in 2022. Results
327 are shown as mean \pm SE

	Bass Rock	Grassholm	Rouzic
Total nb of equipped individuals	10	12	15
Nb of individuals retained	10	5	13
Total nb of foraging trips	310	53	257
Average nb of foraging trips per individual	31 \pm 4	10 \pm 5	20 \pm 3
Total Nb of periods on the colony	49	31	36
Average nb of periods on the colony per individual	30 \pm 4	12 \pm 5	18 \pm 2
Tracking period	11/08/2022 - 12/10/2022	10/08/2022 – 18/09/2022	24/08/2022 – 28/09/2022
Average tracking duration per individual (days)	44.2 \pm 5.1	13.8 \pm 5.8	22.0 \pm 2.4
Maximal distance to the colony (km)	98 \pm 8	65 \pm 8	62 \pm 4
Total distance travelled per trip (km)	254 \pm 21	191 \pm 28	171 \pm 11
Trip duration (h)	19 \pm 2	16 \pm 4	18 \pm 1
Time spent resting during a trip (%)	21.7 \pm 10	23.4 \pm 3.2	42.4 \pm 1.5
Time spent foraging during a trip (%)	54.4 \pm 1.2	55.7 \pm 2.9	36.9 \pm 1.2
Time spent flying during a trip (%)	23.9 \pm 0.8	20.9 \pm 2.2	20.7 \pm 0.9
Time at the colony between at-sea trips (h)	16 \pm 1	18 \pm 2	11 \pm 1

Table 2. Results from the models testing the effects of time (dates between August and October 2022) on northern gannet trip characteristics and nest attendance (linear mixed models) and proportion of time spent in the 3 inferred behavioural states (logistic regressions). Individual identity is included as a random effect. Significant results ($p < 0.05$) are in bold.

	Bass Rock				Grassholm				Rouzic			
	Estimate	df	t or z-	p-	Estimate ±	df	t or z-	p-	Estimate ±	df	t or z-	p-value
					± SE				value			
Maximal distance	0.009 ±	299	2.03	0.043	-0.012 ±	44	-0.85	0.40	-0.003 ±	243	-0.53	0.60
	0.005				0.014				0.006			
Total distance travelled	0.011 ±	299	2.34	0.02	-0.017 ±	44	-1.07	0.29	1.8e10 ⁻⁵ ±	243	0.003	0.99
	0.005				0.016				6.0e10 ⁻³			
Trip duration	0.013 ±	299	3.29	0.001	-0.014 ±	44	-0.74	0.46	0.011 ±	243	1.73	0.09
	0.004				0.019				0.006			
Time at the colony between at-sea trips	-0.003 ±	288	-0.77	0.45	-0.011 ±	56	-1.13	0.26	-0.015 ±	220	-2.09	0.038
	0.003				0.0010				0.007			
Proportion of a trip spent resting	0.0053 ±	307	0.63	0.53	-0.05 ± 0.05	47	-1.18	0.24	0.018 ±	253	1.24	0.21
	0.0086								0.014			
Proportion of a trip spent foraging	-0.0017 ±	307	-0.24	0.81	0.037 ±	47	1.05	0.29	-0.014 ±	254	-0.91	0.36
	0.007				0.034				0.015			
Proportion of a trip spent flying	-0.0028 ±	307	-0.33	0.74	-0.0021 ±	47	-0.05	0.96	-0.008 ±	254	-0.43	0.67
	0.008				0.040				0.018			

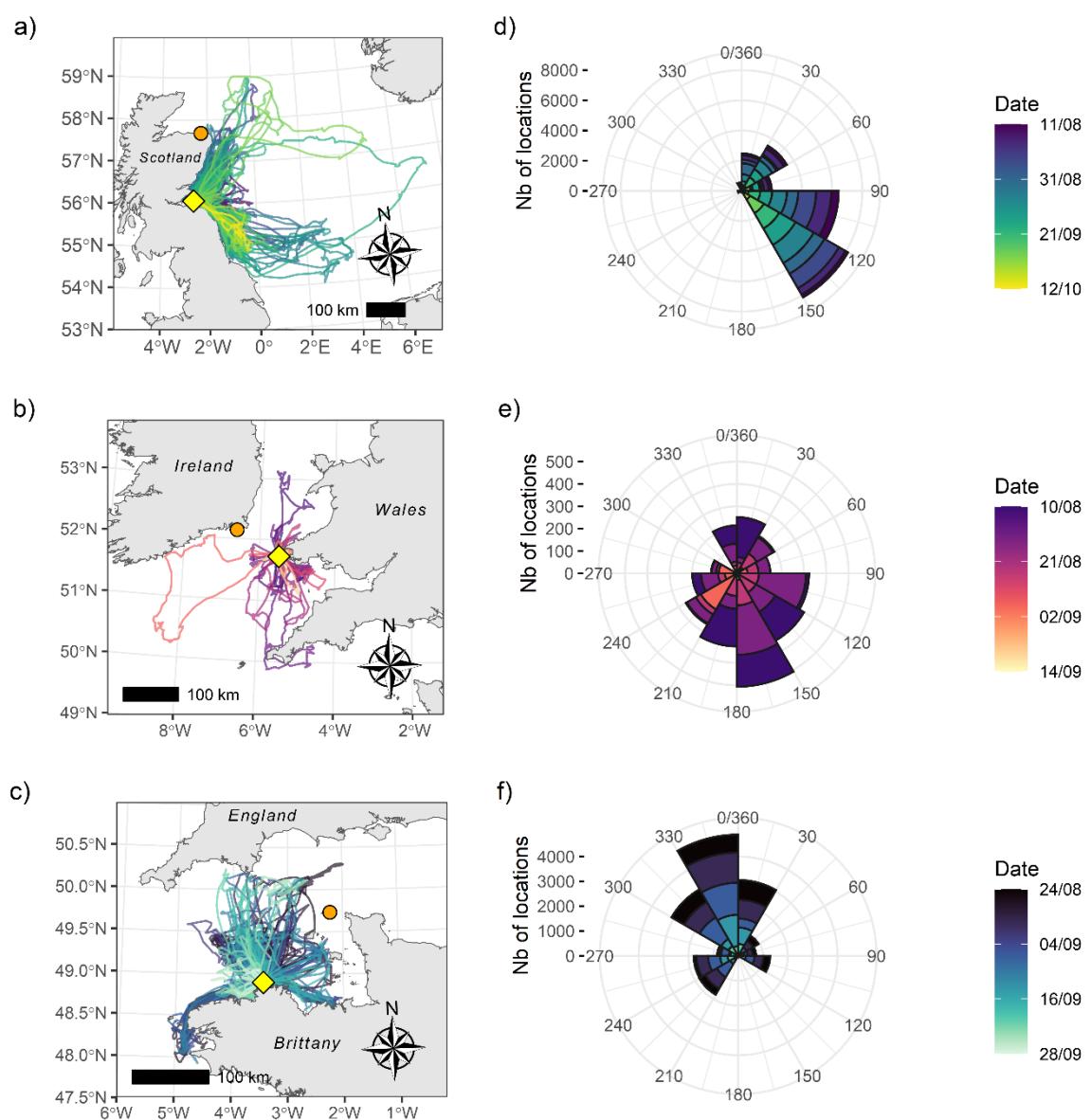


Figure 1. Tracks of northern gannets nesting in 2022 on (a) Bass Rock, Scotland, (b) Grassholm, Wales and (c) Rouzic, Brittany, (yellow diamonds). Orange circles represent the closest neighbouring gannet colony to the respective study colonies. Gradual changes in colour represent time in days since start of GPS tracking. (d-f) Rose diagrams illustrate the bearings of at-sea locations in 30 degree bins. The centre of each rose diagram represents the colony location, the length of each wedge represents the number of locations recorded in that direction over time, in coloured weekly bins.

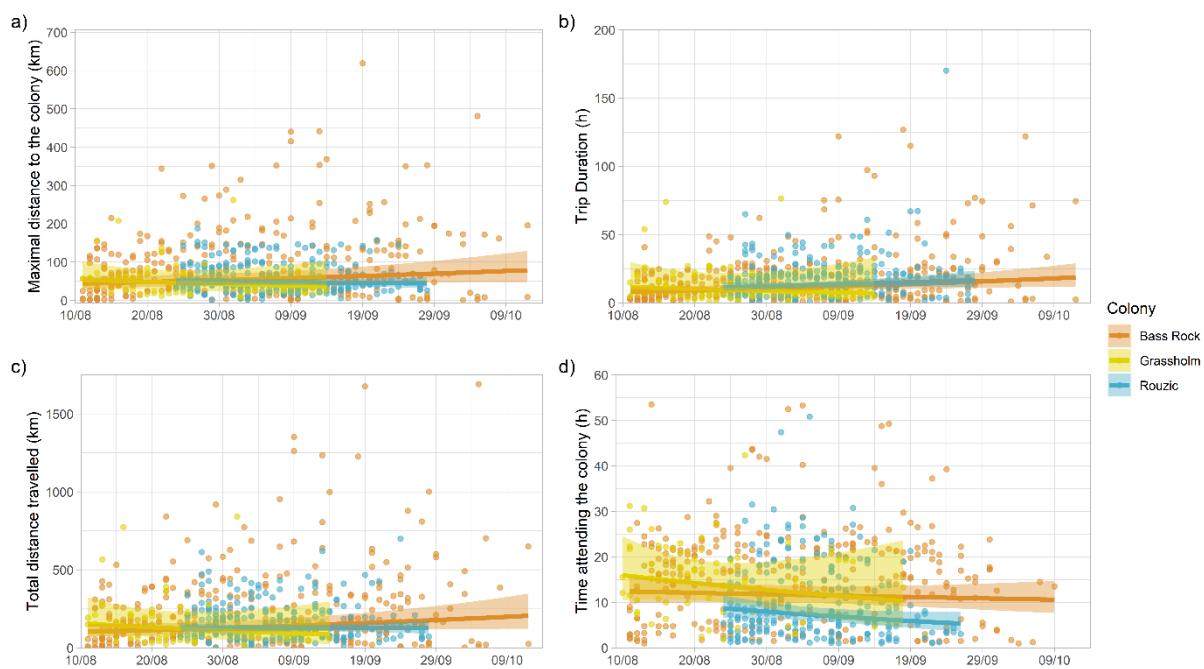


Figure 2. Trip characteristics and nest attendance of northern gannets nesting on Bass Rock (orange), Grassholm (yellow) and Rouzic (cyan), according to dates in August to October 2022. The dots represent raw data and the line and shadow the predicted average slope \pm SE.

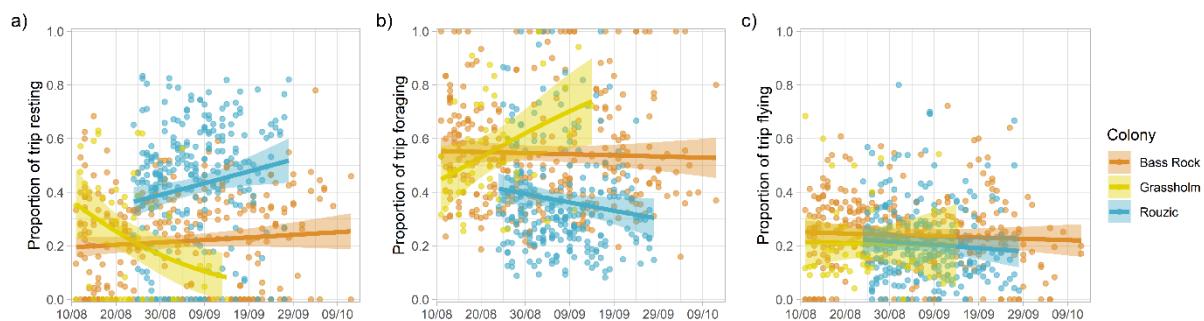


Figure 3. Proportion of inferred behavioural states [(a) resting, (b) foraging, (c) flying] during at-sea trips of northern gannets nesting on Bass Rock (orange), Grassholm (yellow) and Rouzic (cyan), according to dates in August to October 2022. The dots represent raw data and the line and shadow, predicted average slope \pm SE.

Discussion

- Epidemiology

Our analyses confirmed that northern gannets contracted HPAIV, and other investigations also pointed to HPAIV as the cause for 2022 seabird mass-mortalities in western Europe (Falchieri et al., 2022). More specifically, we identified H5N1 (clade 2.3.4.4b) in Rouzic birds. This contrasts with recent HPAIV outbreaks in southern African seabirds (Molini et al., 2020), which were caused by H5N8 (clade 2.3.4.4b). Our study adds to the evidence that HPAIV has become established in seabirds, and will probably recurrently re-emerge, as observed in southern Africa (Molini et al., 2020). We also found that some juvenile gannets had H5N1 antibodies, but no live virus (Suppl. 2). This is in line with recent investigations (Caliendo et al., 2022) suggesting that birds that survived HPAIV develop an immune response, which could protect against future infections. Further longitudinal monitoring will nonetheless be necessary to fully test this hypothesis. Those studies will also clarify the factors leading to intra and interspecific heterogeneity in avian responses to HPAIV (Keawcharoen et al., 2008), which are key to our understanding of the potential role of different species as HPAIV maintenance host or spreaders (Huang et al., 2019).

Only one of the 15 birds equipped with GPS on Rouzic tested HPAIV positive using swab samples (Suppl. 2), and gannets fitted with GPS on Bass Rock and Grassholm could not be tested. Thus, the epidemiological status of most tracked gannets was not known. Ideally, swab and plasma samples should have been collected in all birds. Yet, even in the presence of both sample types, some uncertainty would remain. Notably, a positive plasma sample could reflect a former, rather than an ongoing infection, and such samples are not adequate to infer whether a bird is a HPAIV carrier and potential spreader at the time of the blood sample. Indeed, experimentally infected birds stop excreting the virus after a week or less (van den Brand et al., 2018). Swab samples are therefore theoretically adequate during this brief excretion period, but half of those for gannets equipped with GPS on Rouzic were inconclusive. Overall, we may therefore conclude that HPAIV was extremely widespread and circulating at all three gannet colonies given observational data on the degree of mortality, and that an unknown proportion of GPS-tracked birds could have been symptomatic or asymptomatic carrier of the virus. This knowledge gap clearly calls for further epidemiological studies during future seabird breeding seasons.

- Movement ecology

We did not detect any change in breeding colony fidelity in the context of HPAIV outbreaks that started approximately two months previous to data collection. None of the tracked gannets came ashore outside of their respective breeding colonies while alive. We also found that GPS-tracked gannets did not significantly modify their foraging patterns across the study period (Table 2; Fig. 1-3). Since our visits to gannet breeding colonies were extremely limited due to the restrictions in place, we could not monitor the survival of the chicks of the GPS-tracked gannets. Some birds may have lost their chicks during the study period. Yet, all tracked birds continued to regularly commute between at-sea feeding sites and their respective colonies, and none of them rested on the mainland or on other islands in-between trips.

Further, gannet foraging effort seemed lower than during the 2019 breeding season (hence before HPAIV) at our three study sites (Grémillet et al., 2006; Hamer et al., 2007; Patrick et al., 2014) (Suppl. 4). Therefore, gannets surviving HPAIV may have benefited from relaxed density-dependence. Our data are not directly comparable with those collected in 2019, because we studied the late chick-rearing period of the birds, whereas most previous studies focused on early chick-rearing. Yet, late chick-rearing requires twice more energy than early chick-rearing (Montevecchi et al., 1984), and lower foraging effort during late chick-rearing in 2022 does point to reduced intra- and interspecific competition for food.

Our results are coherent with high breeding and foraging site fidelity in colonial seabirds (Danckwerts et al., 2021), and contrary to the idea that gannets that have witnessed and survived mass mortality at their breeding colony modify their movement patterns as a consequence of the disease outbreak and maintain these changes several months after the event. Thus, it appears that the capacity for long-term enhanced HPAIV transmission throughout the metapopulation and potentially throughout the co-existing seabird populations is low for adult breeding gannets. This is an essential piece of information that contributes to a better understanding of HPAIV transmission dynamics, since wild birds carrying HPAIV are recurrently presented as virus spreaders to farm poultry (H5N8 and Viruses, 2016, p. 8).

However, the data we presented here are collected following the initial disease outbreak to study long-term behavioural responses, and they are only representative of the adult breeding

age class. Short-term responses of breeding birds, at the start of a disease outbreak, might differ from the behavioural and spatial consistency we demonstrated here. It might also be that age classes differ in their propensity to act as a vector for HPAIV. Immature gannets have been shown to perform visits to other breeding colonies throughout the breeding season (Votier et al., 2011) and thus likely regularly move between colonies. These prospecting movements would appear to require limited time/energy investment: For gannets from Bass Rock, the closest alternative colony is Troup Head on the Scottish mainland (ca. 210 km), for Grassholm it is Great Saltee in Ireland (ca. 90 km), and for Rouzic it is Ortac in the British Channel Islands (ca. 130 km) (Fig.1). Reaching these neighbouring colonies would take 3.2 hrs (Bass Rock), 1.4 hrs (Grassholm), or 2 hrs (Rouzic), assuming a 65 km.h^{-1} travelling speed (Grémillet et al., 2004). Forthcoming studies will clarify the respective potential of juvenile and immature gannets to act as vectors in HPAIV transmission. Also, even if rated as rare (Boulinier et al., 2016), at-sea HPAIV transmission may occur within, and between seabird species. This might be facilitated by aggregations at natural foraging sites or whilst feeding on fishery wastes behind trawlers, or through kleptoparasitism and scavenging (Wille et al., 2016). Studying interspecific fine scale space-use overlap at sea is therefore a worthwhile avenue for future monitoring and evaluation of disease transmission scenarios (Boulinier, 2023).

- Outlook

It remains unclear how gannets contracted HPAIV, since they were either at sea, or at their breeding colony during the outbreak. Larids (*Larus sp.*) or great skuas that klepto-parasitise gannets might be potential vectors since they use similar terrestrial and marine habitats (Falchieri et al., 2022), but further analyses will be necessary to test these hypotheses. HPAIV first affected gannets in Iceland, Québec and Scotland (from early April 2022), and subsequently arrived in Brittany (from early July 2022). Hence, it is possible that gannets moving between these colonies may have spread the virus, but this pathway is still hypothetical. Equally unknown are HPAIV dynamics during gannet migration, which started in September-October 2022 and lasted until February 2023. These inter-breeding movements take gannets from the British Isles and Brittany to the Mediterranean or West Africa (Fort et al., 2012). Off Africa, gannets meet with some of their North American conspecifics, as well as

with a vast community of North Atlantic seabirds spending the winter in tropical waters (Grecian et al., 2016).

Our study is a key example of the common fate of wildlife and humanity facing global changes (Díaz et al., 2019). Gannets are affected by the direct and indirect consequences of climate change (heat waves and storms, changes in the distribution and abundance of marine resources), by pollutions (e.g. mercury in fish affecting seabird and human health), and by uncontrolled fishing operations which threaten food security for seabird and human populations alike (Grémillet et al., 2020). In addition, the current HPAIV outbreak demonstrates that the anthropogenic environmental crisis enhances the potential for emerging infectious disease, contaminating wild animals and humans (Carlson et al., 2022; Kuiken and Cromie, 2022). Indeed, current industrial farming practices are responsible for the emergence and the spread of HPAIV in poultry and subsequently in wild birds, potentially also in humans (Yamaji et al., 2020).

Declarations:

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Author contributions: DG, PP and SCV designed the study, with advice from SW and JJ. DG, PP, APr, TP, JJ, SCV, JM, AB, JF, NC, RJ, LL, AT, NS and JL were leading the field studies including

funding acquisition, permit acquisition and field data collection. APo, PP, MA-Z, AG, NC and DG analysed the data. DG, APo, AG and JJ wrote the paper, with inputs from all other authors.

Conflicts of interests: the authors declare no conflicts of interests

Ethics: All procedures followed the *guidelines for the treatment of animals in behavioural research and teaching* of the *Association for the Study of Animal Behaviour*. Bass Rock: fieldwork was performed in partnership with the Scottish Seabird Centre with permission of the landowner of the Bass Rock, Sir Hew Dalrymple, and under a special method endorsement and ringing permit of the British Trust for Ornithology BTO to Jana Jeglinski. Colour ringing was performed under a permit to Jude Lane from the BTO. We conducted our fieldwork under an exemption to the general ringing ban in seabird colonies granted by NatureScot which permitted us to capture and tag gannets during the HPAIV outbreak. All fieldwork was performed with the required risks assessments and ethical approval in place. Grassholm: All research was carried out under licence (RSPB, Natural Resources Wales (#S091127-1), British Trust for Ornithology (BTO: A4257), the BTO Special Methods Panel and the UK Home Office (30/3065). Rouzic: fieldwork operated under the Programme Personnel de baguage n°536 CRBPO/MNHN validation 2020-2024.

Data availability: Data are available on the following archives:
https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2296851236 ;
<https://datadryad.org/stash/share/MmNkFWcQV79wnYDMQ8VTav-jRmHBUomyRohKVoAsNvE> and
https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2658117564. All statistical analyses can be found on the GitHub repository (<https://github.com/auponchon/NorthernGannets2022>).

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