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

3

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29 Abstract:

30 High pathogenicity avian influenza virus (HPAIV) caused the worst seabird mass-mortalities in  
31 Europe across 2021-2022. The northern gannet (*Morus bassanus*) was one of the worst  
32 affected species, with tens of thousands of casualties in the northeast Atlantic between April-  
33 September 2022. Disease outbreaks can modify the movement ecology of animals by  
34 diminishing spatial consistency, thereby increasing the potential for disease transmission. To  
35 detect potential changes in movement behaviour, we GPS-tracked breeding adults following  
36 the initial HPAIV outbreak, at three of the largest northern gannet breeding colonies where  
37 major mortality of adults and chicks occurred (Bass Rock, Scotland, UK; Grassholm, Wales,  
38 UK; Rouzic, Brittany, France). We also gathered background epidemiological information and  
39 northern gannet colony dynamics during the outbreak. Our data indicate that HPAIV killed at  
40 least 50% of northern gannets, and suggest the presence of HPAIV H5N1 antibodies in  
41 juveniles. GPS-tracked adult northern gannets remained faithful to their breeding sites  
42 despite the HPAIV outbreak and did not prospect other breeding colonies. They performed  
43 regular foraging trips at sea, similar to their behaviour before the outbreak. Comparison with  
44 GPS-tracking data gathered in 2019, i.e. before the HPAIV outbreak, suggested lower foraging  
45 effort in birds which survived HPAIV in 2022, potentially as a consequence of reduced intra-  
46 and interspecific food competition. Breeding colony fidelity of surviving adult northern  
47 gannets following HPAIV mass-mortalities indicates limited capacity for viral spread during  
48 our study. This may contrast with the behaviour of adults during the initial disease outbreak,  
49 and with that of younger individuals.

50

51 Keywords: Avian pathogens, Behavioural latency, Human/wildlife interaction, Movement  
52 ecology, Seabird conservation, Viral transmission

53

## 54 Introduction

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

70 This is the case for seabirds, which are currently the most endangered bird group apart from  
71 parrots (Phillips et al., 2023). Half of the worldwide abundance of seabirds has been lost since  
72 1970 (Grémillet et al., 2018), mainly because of breeding habitat loss, mortality caused by  
73 fishing gear, invasive species (e.g. cats and rats), food competition with fisheries, direct and  
74 indirect consequences of climate change, and pollution (Young and VanderWerf, 2023).  
75 Pathogens can also have significant impacts on seabird populations, as demonstrated by the  
76 effects of avian cholera (*Pasteurella multocida*) on Cape cormorants (*Phalacrocorax capensis*)  
77 in South Africa (Crawford et al., 1992), and on common eiders (*Somateria mollissima*) in North  
78 America (Iverson et al., 2016). While seabirds are common hosts of low pathogenicity avian  
79 influenza viruses (LPAIV) (Lang et al., 2016), HPAIV had rarely been detected before the 2021-  
80 2022 outbreak, except in Southern Africa where recurrent HPAIV outbreaks have affected  
81 seabirds since 2016 (Molini et al., 2020). Now, for the first time, HPAIV is significantly affecting  
82 European seabird populations, with the virus spreading to 12 species in the UK (Falchieri et  
83 al., 2022). Tens of thousands of seabirds are thought to have been affected in the Northeast  
84 Atlantic in 2022, with northern gannets (*Morus bassanus*; hereafter gannets) among the most

85 severely impacted species (Lane et al., 2023), together with great skuas (*Stercorarius skua*)  
86 (Banyard et al., 2022) and sandwich terns (*Thalasseus sandvicensis*) (Rijks et al., 2022).  
87 Gannets are an iconic species that attract conservation and media interest, in their own right,  
88 but also as umbrella species for the marine environment. Despite living in some of the most  
89 anthropogenically modified marine regions of the planet (e.g. the North Sea), gannet  
90 populations consistently increased across their distribution zone in the northeast Atlantic  
91 during the second half of the 20<sup>th</sup> century (Grandgeorge et al., 2008).

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

104 However, dense seabird colonies also function as information centres (Evans et al., 2016)  
105 where birds acquire public information from their conspecifics, such as the location of  
106 potential food resources at sea (Courbin et al., 2020), or the quality of local breeding habitats  
107 (Danchin et al., 1998). During the 2022 HPAIV outbreak, when many chicks and adult gannets  
108 died at breeding colonies, surviving adult gannets were exposed to public information  
109 signalling that they were breeding in a highly hazardous habitat. As an effect of such  
110 disturbance, we might expect to see drastic changes in movement and space use patterns.  
111 Indeed, recent work has shown that surviving adults gannets that had lost their chick and  
112 partner drastically modified their movement patterns in May/June 2022, during the initial  
113 phase and peak of the HPAIV outbreak on the Bass Rock (Jeglinski et al., 2023): Birds thereby  
114 switched from exclusively commuting between their nest and foraging areas at sea, to visiting  
115 other breeding colonies. Such changes in movement patterns increase the potential for

116 disease transmission, by increasing the likelihood of contact, be it on land or at sea, between  
117 birds from different colonies (Boulinier, 2023; Boulinier et al., 2016).

118 However, it is unclear if the behavioural responses to the initial HPAI outbreak found by  
119 Jeglinski and colleagues (2023) translate to longer term and more permanent modifications  
120 in movement ecology and space use of surviving gannets. For example, seabird mass-  
121 mortalities are likely to reduce food competition for surviving individuals and may therefore  
122 lead to modified foraging patterns and changes in at-sea distribution of gannets which are  
123 relevant for the conservation management of the species. Short-term effects on movement,  
124 such as the increase in adult prospecting frequency described above, could become a more  
125 permanent feature. This would lead to increased connectivity between usually segregated  
126 breeding colonies and thus have the potential to maintain enhanced disease transmission,  
127 within gannet metapopulations and at the scale of multispecies seabird communities  
128 (Boulinier et al., 2016). Finally, survivors could abandon their breeding colony permanently,  
129 as shown in Cape cormorants or Double-crested cormorants (*Phalacrocorax auritus*) which  
130 desert breeding colonies when exposed to avian cholera or Newcastle disease virus (Crawford  
131 et al., 1992; Leighton et al., 2021). It is uncertain whether gannets display such longer-term  
132 behavioural shifts, because they are known for their high fidelity to nesting (Nelson, 1966),  
133 and foraging sites (Votier et al., 2017; Wakefield et al., 2015). Also, studies on closely-related  
134 Cape gannets (*Morus capensis*) showed that, even when confronted with strongly degraded  
135 environmental conditions, adult breeders kept the same breeding and foraging locations  
136 (Grémillet et al., 2016; Pichegru et al., 2010).

137 Previous investigations showed that, in Indian yellow-nosed albatrosses (*Thalassarche*  
138 *carteri*) exposed to avian cholera, failed breeders showed higher flexibility in habitat use  
139 (Ponchon et al., 2021). Yet, to the best of our knowledge, no study has investigated seabird  
140 movements following an HPAIV outbreak, and very few have done so in other birds (Gaidet  
141 et al., 2010), generally because of the unpredictability of outbreaks and restrictions regarding  
142 colony access in an HPAIV context. We used the rare opportunity to fill this critical knowledge  
143 gap by collecting data in three of the largest gannet breeding colonies in the Northeast  
144 Atlantic which all experienced very high levels of HPAIV-related chick and adult mortality in  
145 2022; the Bass Rock in Scotland (UK), Grassholm in Wales (UK), and Rouzic in Brittany (France).  
146 Bass Rock was, before the HPAIV outbreak, the largest northern gannet colony in the world,

147 with an estimated 75,259 breeding pairs (Murray et al., 2014). Taken together, the three  
148 studied colonies totalled ca. 26% of the northern gannet world population (134,259 out of  
149 525,694 pairs (Murray et al., 2015)).

150 Our primary objective was to better understand the effect of the HPAIV outbreak on breeding  
151 gannet space use, since potential persistent behavioural shifts may maintain a high degree of  
152 transmission potential in the metapopulation (Boulinier, 2023). Specifically, we tested the  
153 hypothesis that gannets which survived the initial HPAIV outbreak modified their movement  
154 patterns relative to their behaviour prior to the outbreak. We predicted (1) that surviving  
155 birds would prospect for alternative breeding sites and (2) they also modified their foraging  
156 patterns in response to the reduction of food competitors.

157 Our second objective was to provide background epidemiological information, and data on  
158 gannet colony dynamics in our three study colonies during the outbreak. The HPAI outbreak  
159 disrupted ecological data collection in seabird colonies in 2022. Consequently, there are very  
160 limited ecological and epidemiological insights based on field data available, making it  
161 paramount to share contextual information with the scientific community.

162

## 163 Methods

164 Gannets were primarily studied in May-October 2022 on Bass Rock, Scotland (56°04'N,  
165 2°29'E), Grassholm, Wales (51°43'N, 05°28'W), and Rouzic, Brittany (48°54'N, 3°26'W).  
166 Gannet spatial ecology was also compared between 2022 and 2019 (i.e. before the HPAIV  
167 outbreak). Gannets breed between February and October, with peak hatching during the first  
168 half of June. Time of hatching is influenced by latitude, with median hatching occurring on  
169 average two weeks later on Bass Rock than on Grassholm and Rouzic (Wanless et al., 2008).  
170 The chick-rearing phase lasts 11 to 12 weeks, with chicks fledging from late August to early  
171 October. All personnel involved in field operations were equipped with full-body suits and  
172 disposable gloves, face masks, goggles and caps. Biocides (Virkon® or SafeFour®) were used  
173 between each manipulated bird to clean clothing, shoes and equipment.

174

175 Characterization of the HPAIV outbreak:

176 - Bass Rock:

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

180 - Grassholm:

181 Following an unusually high number of dead gannets at the colony, HPAIV was confirmed  
182 from Grassholm on 3<sup>rd</sup> August with no further access to site permitted for the rest of the  
183 breeding season.

184 - Rouzic:

185 Mortality affecting adult gannets was first recorded on 1<sup>st</sup> July 2022 on the live camera  
186 monitoring the Rouzic colony. Samples were subsequently collected from 31 live or dead  
187 gannets in, and around the Rouzic colony between July and September 2022, for HPAIV  
188 screening and characterization. We performed opportunistic necropsies on four adult birds  
189 found dead on the colony, from which we collected tracheal and cloacal swabs and/or lung  
190 and trachea samples. We also collected cloacal swabs, tracheal swabs and/or external wipes  
191 impregnated with sterile distilled water (applied to the feathers and featherless areas of the  
192 birds) from live individuals showing no HPAIV symptoms, including 15 adult birds equipped  
193 with GPS-GSM loggers (see below), and 12 recently fledged juvenile birds captured at sea or  
194 in the colony. We also collected plasma samples from seven of these juvenile birds. All  
195 samples were stored at -20°C until laboratory analyses.

196 Samples were analysed using the protocols recommended by the French Ministry of  
197 Agriculture and based on the recommendations provided by the OIE/FAO international  
198 reference laboratory for avian influenza. Tissue and swab samples were screened for HPAIV  
199 genetic material by real-time reverse transcription polymerase chain reaction (rRT-PCR)  
200 targeting the M gene. To identify the subtype of the circulating virus, positive samples were  
201 then typed using an rRT-PCR targeting either the H5 or H7 type of the haemagglutinin gene.  
202 One sample testing positive for H5 was analysed for further characterization of the virus with  
203 an RT-PCR discriminating HP H5 of the 2.3.4.4b clade, and an RT-PCR targeting the N1 type of  
204 the neuraminidase gene. Samples testing negative for host genetic material were classified as  
205 potential false negative (Zhang et al., 2020), likely due to the degradation of the samples, and



206 were excluded from the study. Plasma samples were screened for antibodies specifically  
207 targeting H5N1, H5N3, H5N5 or H5N8 by haemagglutination inhibition (HI). Collected samples  
208 and associated laboratory results are summarized in Table S2 (Suppl. 2).

209

210 GPS tracking:

211 Gannets were tracked (1) ~ 2 months following the first signs of an HPAIV outbreak in each  
212 respective colony in 2022. This period, spanning mid-August to early October 2022,  
213 corresponded to the late chick-rearing phase. This information was compared with (2) GPS  
214 tracking data collected in 2019, a normal year prior to the occurrence of HPAIV in gannets.  
215 For logistical reasons, this second data set was collected during June-July 2019, a period  
216 corresponding to early chick-rearing. Since gannet foraging effort may differ between early  
217 and late chick-rearing this comparison requires some caution. Notably, because chick energy  
218 requirements double between early and late chick-rearing (Montevicchi et al., 1984), and  
219 because food resources may become depleted around seabird colonies at the end of the  
220 breeding season (Weber et al., 2021), adult gannet foraging effort should increase between  
221 early and late chick-rearing.

222 (1) To study gannet movement ecology following the initial HPAIV outbreak, we deployed  
223 GPS-GSM tags on breeding adults which showed no HPAIV symptoms on the Bass Rock (10  
224 birds between 11<sup>th</sup> - 13<sup>th</sup> August 2022) and on Rouzic (15 birds between 23<sup>rd</sup> - 26<sup>th</sup> August  
225 2022). GPS-GSM tags were pre-programmed to send data to a server using the 2G mobile-  
226 phone network so that data can be transmitted from anywhere within 2G coverage and  
227 accessed by the user in near-real-time. At Grassholm, 11 birds had been fitted with remotely-  
228 downloadable tags that send data via a UHF link to a base station deployed at the breeding  
229 colony, in May 2022, prior to the HPAIV outbreak. Some of these tags were still functional  
230 across August-September 2022.

231 For all GPS deployments, adults rearing chicks (2 to 8 weeks old) were caught at the nest and  
232 handled so as to minimize stress: the procedure lasted < 10 min and birds were kept in the  
233 shade. Tags were attached with Tesa® tape to the three central tail feathers. For Bass Rock  
234 gannets, we used nanofix tags (Pathtrack Ltd., solar powered, mass 18 g, 0.7% of bird body  
235 mass, dimensions 56x28x15mm plus ~40 mm external whip antenna). For Grassholm gannets,

236 we used axy-trek remote tags (Technosmart solar powered, mass 15 g, < 0.5% of bird body  
237 mass, dimensions 52x25x15 mm). For Rouzic gannets, we used OrniTrack-9 tags (Ornitela,  
238 solar powered, mass 9 g, 0.3% of bird body mass, dimensions 37x19x12 mm, plus ~10 cm  
239 external whip antenna). All tags recorded a GPS position every 15 to 60 min, depending on  
240 battery voltage. We planned for tags to fall off once birds were starting to moult their tail  
241 feathers - previous deployments lasted up to 3 - 5 months (J. Jeglinski, D. Grémillet,  
242 unpublished data). At all three colonies we weighed gannets to the nearest 10 g. All birds  
243 were ringed with a metal ring and plastic ring with a unique alphanumeric combination. Once  
244 released, most birds returned immediately to their nests. We monitored chicks until the  
245 captured parent had returned, generally immediately, at the latest within 1 h after capture.

246 (2) We studied the movements of breeding adult gannet before the HPAIV outbreak, during  
247 early chick-rearing in June-July 2019. We used the same methodology as above, yet slightly  
248 different GPS recorders. On Bass Rock, 22 gannets were fitted with i-gotU GT600 tags (Mobile  
249 Action Technology, mass 30g, 1% of body mass, dimensions 47 × 30 × 20 mm, set to record  
250 GPS position every 1 min). On Grassholm 7 gannets were fitted with i-gotU GT120 tags  
251 (Mobile Action Technology, mass 18g, 0.7% of body mass, dimensions 47 × 30 × 20 mm, set  
252 to record GPS position every 1 min). On Rouzic, 14 gannets were fitted with CatTraQ™ tags  
253 (Catnip Technologies, mass 20g, 0.8% of bird body mass, dimensions 47 × 30 × 13 mm, set to  
254 record GPS position every 1 min).

255 GPS Data processing:

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

259 For all tracking data recorded in 2022 and 2019 (Tab. 1), at-sea trips were discriminated from  
260 periods in the colony when the birds were > 1 km away from the colony for > 1 h. GPS  
261 recordings which were interrupted for > 10 hours were excluded. At-sea locations were  
262 linearly interpolated with a 15 min time resolution using the *pastecs* package (Grosjean et al.,  
263 2018). Trip data were checked for prospecting visits to other gannet colonies, which we  
264 defined as two or more consecutive locations in any other gannet known colony.

265 We calculated trip characteristics for the 2019 and 2022 data sets (maximal distance to the  
266 colony, total trip duration and total distance travelled), as well as the time spent in the colony  
267 between at-sea trips, and presented these averaged for each individual and then averaged by  
268 colony in Table 1. Further, we fitted linear mixed models on each colony separately to test  
269 whether log-transformed trips characteristics and colony attendance changed significantly  
270 between 2022 and 2019.

271 To test our hypotheses, we were specifically interested in temporal dynamics of foraging  
272 patterns following the HPAIV outbreak. Hence, for the 2022 data set, we fitted linear mixed  
273 models separately for each colony using the respective trip characteristics for each bird as  
274 response variables to test whether log-transformed trip characteristics and time spent in the  
275 colony between at-sea trips changed significantly over time (converted as day since 10<sup>th</sup>  
276 August 2022, first day of the study period). Bird ID was included as a random effect.

277 Inferring at-sea behavioural states:

278 To test for temporal dynamics in behavioural patterns across the 2022 data set, we also fitted  
279 a 3-state hidden Markov model (HMM) to the at-sea interpolated location data from all three  
280 colonies combined, using the *moveHMM* package (Michélot et al., 2016). The states can be  
281 interpreted to reflect three different activities at sea: (1) resting, characterised by a small step  
282 length and low turning angle, (2) travelling, characterised by a long step length and low  
283 turning angle and (3) foraging, characterised by an intermediate step length and a large  
284 turning angle. A set of different initial parameter values was used to ensure that the global  
285 maximum log-likelihood had been reached. The Viterbi algorithm was used to classify the  
286 most likely behaviour at each location and proportions of each activity occurring during one  
287 at-sea trip were calculated, averaged by individual and then, by colony. We then fitted logistic  
288 regressions to the proportions of each activity during a trip for each bird as response variables  
289 using the *glmmTMB* package (Brooks et al., 2017), accounting for zero-inflated data, to test  
290 whether activity proportions changed over time (converted as day since 10<sup>th</sup> August 2022,  
291 first day of the study period). Bird ID was included as a random effect.

292

293 Results:

294 Gannet colony dynamics:

295 The impact of HPAIV on the Bass Rock was extremely high, with thousands of dead gannets  
296 recorded in the colony and washed up on the surrounding beaches. A drone survey on 30<sup>th</sup>  
297 June 2022 counted 21,277 gannets (Lane et al., 2023), whereas a previous census counted  
298 75,259 apparently occupied sites (AOS) in 2014 (Murray et al., 2015). Although the two counts  
299 use different count units, they indicate a substantial decline in numbers of around 70% during  
300 the 2022 HPAIV outbreak (Lane et al., 2023). Direct observations on Bass Rock also indicated  
301 that at least 75% of active nests disappeared during the 2022 breeding season (Lane et al.,  
302 2023). On Grassholm, adult and chick mortality were extremely high with many thousands of  
303 birds dead on the colony and in the surrounding waters. On Rouzic, aerial pictures of the  
304 colony revealed that AOS numbers declined from 18,839 on 17/05/2022, to 8,625 on  
305 28/08/2022 (54% decline during the breeding season). Observations via the live camera  
306 installed on the breeding colony estimated that >90% of chicks died during the same period  
307 (Suppl. 1). More detailed, weekly counts performed between 11/07/2022 and 30/09/2022 on  
308 five sections of the colony containing 40-102 AOS, suggested that between 58-87% of  
309 breeding adults, and between 67-94% of the chicks died (see Suppl. 4).

310

311 Characterization of the HPAIV outbreak

312 - Bass Rock:

313 Samples collected on the 4<sup>th</sup> June 2022 from dead gannets and analysed by the Animal and  
314 Plant Health Agency (APHA), UK, confirmed an outbreak of HPAIV H5N1 (Scottish Seabird  
315 Centre, pers. comm.).

316 - Grassholm:

317 Following unusual gannet mortality in late July, four birds found dead on 21<sup>st</sup> July 2022 were  
318 confirmed as positive for HPAIV H5N1 by APHA.

319 - Rouzic:

320 The first necropsy samples collected from a dead adult found on the colony on 11<sup>th</sup> July 2022  
321 tested positive for HPAIV. Laboratory analyses conducted on samples collected from a bird

322 found dead on the colony on 30<sup>th</sup> September 2022 confirmed the circulation of HPAIV H5N1  
323 clade 2.3.4.4b in the colony. HPAIV H5 was also detected in live birds: 1/9 cloacal swabs from  
324 adults subsequently equipped with GPS, and 2/7 external wipes from juveniles (recently  
325 fledged and captured on land/at sea) tested positive for HPAIV H5. All the cloacal and tracheal  
326 swabs collected from these juveniles, as well as from 5 other juveniles were classified as  
327 negative or inconclusive, suggesting varying detection probabilities across sample types (see  
328 Suppl. 2). Antibodies against H5N1 were detected in 4/7 juveniles (including the 2 with RT-  
329 PCR-positive external swipes). These individuals also tested positive for antibodies against  
330 H5N5 and H5N8, and to a lesser degree, for antibodies against H5N3, although higher titers  
331 were systematically observed for H5N1 (Suppl. 2), suggesting cross-reactions with other  
332 serotypes. None of the samples tested positive for HPAIV H7.

333

334 Movement ecology:

335 All 10 GPS tags deployed on Bass Rock gannets in 2022 sent GPS positions. On Grassholm, 5  
336 out of the 11 tags which had been deployed in May 2022 provided data during the study  
337 period (see Table 1 for details). Of the 15 tags deployed on Rouzic, 14 provided data; 13 of  
338 the 15 remained in the English Channel. One gannet, sampled at tag deployment, tested  
339 positive to HPAIV and never provided GPS positions, and another (tested negative at tag  
340 deployment) initiated migration after being equipped, moving toward West Africa without  
341 touching land until the tag stopped sending data on 16<sup>th</sup> November 2022 (Table 1). Average  
342 gannet body mass was 3230±298g (Bass Rock), 3004±325g (Grassholm), and 2920±240g  
343 (Rouzic), values which were similar to those in previous years (Le Bot et al., 2019).

344 While alive, none of the gannets tagged in 2022 came ashore anywhere outside of their  
345 respective breeding colonies during the GPS data transmission period. Overall, gannets from  
346 Bass Rock, Grassholm and Rouzic did not change their space use across the 4-8 week 2022  
347 study period, and foraged consistently in the same areas (Fig. 1 & 2). Birds from Rouzic did  
348 not change their at-sea trip characteristics during the 2022 study period (similar duration,  
349 maximal distance to the colony and total distance travelled; Table 2; Fig. S3a-c), but they  
350 slightly decreased the time spent at the colony between at-sea trips (Table 2; Fig. S3d). Among  
351 them, one individual was found dead on a beach on the island of Guernsey (82 km Northeast

352 of Rouzic), 14 days after being equipped. This individual was not tested for HPAIV when found  
353 dead, and its behaviour for the time period during which we received GPS data did not differ  
354 from that of other Rouzic birds we tracked. During the 2022 study period, birds nesting on  
355 Bass Rock spent the same amount of time attending their colony but increased the duration  
356 of their at-sea trips marginally, travelling slightly further and being absent from the colony for  
357 slightly longer (Table 2; Fig. S3). During the same period, birds from Grassholm did not change  
358 any trip characteristics nor their nest attendance patterns. Considering their activity budgets  
359 during trips, birds maintained the same proportions of time spent foraging, flying and resting  
360 on the water, regardless of their colony (Table 2; Fig. 3). For the 3 colonies, compared to early  
361 chick-rearing in 2019, at-sea trips in 2022 were 47-58% shorter in maximal distance and total  
362 distance travelled and 10-53% shorter in duration (Table 1; S3). Overall, foraging effort as  
363 conveyed through foraging trip indicators was significantly lower in 2022 compared to 2019,  
364 except for foraging trip duration in Rouzic gannets (Fig. 4; Table S3).

365

366 **Table 1.** Details of the GPS tracking data set for gannets nesting on Rouzic, Grassholm and  
 367 Bass Rock in 2022 and 2019. Results are shown as mean  $\pm$  SE

368

	Bass Rock	Grassholm	Rouzic	Bass Rock	Grassholm	Rouzic
	2022			2019		
<b>Total nb of equipped individuals</b>	10	12	15	22	7	14
<b>Nb of individuals retained</b>	10	5	13	22	7	14
<b>Total nb of foraging trips</b>	310	53	257	66	11	27
<b>Average nb of foraging trips per individual</b>	31 $\pm$ 4	10 $\pm$ 5	20 $\pm$ 3	3.0 $\pm$ 0.3	1.5 $\pm$ 0.3	1.9 $\pm$ 0.3
<b>Total Nb of periods on the colony</b>	49	31	36	6	0	7
<b>Average nb of periods on the colony</b>	30 $\pm$ 4	12 $\pm$ 5	18 $\pm$ 2	1.8 $\pm$ 0.3	-	2.9 $\pm$ 0.3

<b>per individual</b>						
<b>Tracking period</b>	11/08/2022 - 12/10/2022	10/08/2022 - 18/09/2022	24/08/2022 – 28/09/2022	23/06/2019 - 30/07/019	15/07/2019 - 17/07/2019	21/06/2019 – 28/06/2019
<b>Average tracking duration per individual (days)</b>	44.2 ± 5.1	13.8 ± 5.8	22.0 ± 2.4	4.8 ± 0.5	1.6 ± 0.4	4.2 ± 0.5
<b>Maximal distance to the colony (km)</b>	98 ± 8	65 ± 8	62 ± 4	186 ± 25	147 ± 18	127 ± 12
<b>Total distance travelled per trip (km)</b>	254 ± 21	191 ± 28	171 ± 11	450 ± 60	450 ± 78	328 ± 35
<b>Trip duration (h)</b>	19 ± 2	16 ± 4	18 ± 1	27 ± 3	34 ± 8	20 ± 2
<b>Time spent resting during a trip (%)</b>	21.7 ± 10	23.4 ± 3.2	42.4 ± 1.5	-	-	-
<b>Time spent</b>	54.4 ± 1.2	55.7 ± 2.9	36.9 ± 1.2	-	-	-



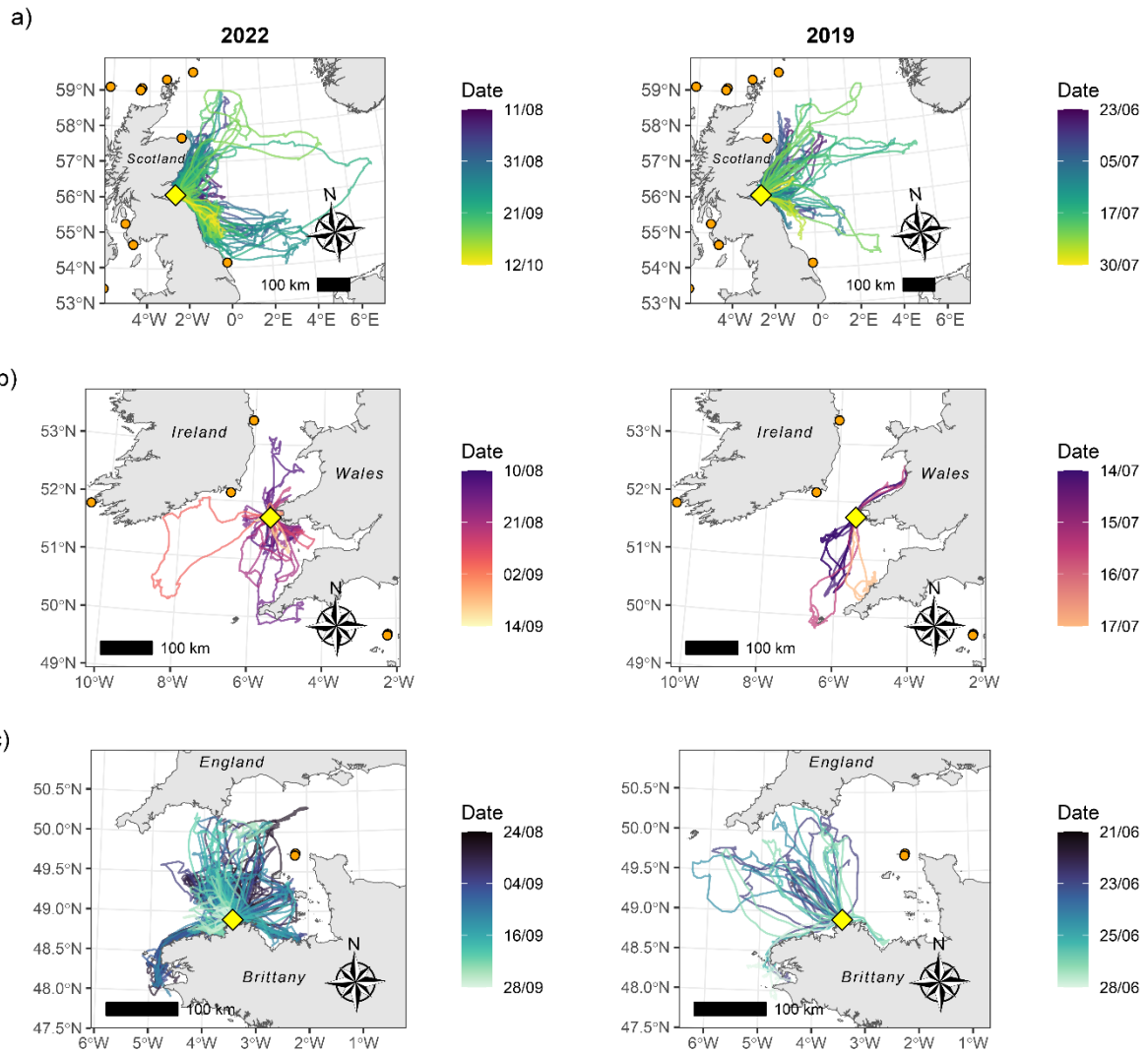
<b>foraging during a trip (%)</b>						
<b>Time spent flying during a trip (%)</b>	23.9 ± 0.8	20.9 ± 2.2	20.7 ± 0.9	-	-	-
<b>Time at the colony between at-sea trips (h)</b>	16 ± 1	18 ± 2	11 ± 1	26 ± 2	-	22 ± 2

370 **Table 2.** Results from the models testing the effects of time for the 2022 data set, on gannet trip characteristics and nest attendance (linear  
371 mixed models) and proportion of time spent in the 3 inferred behavioural states (logistic regressions). Individual identity is included as a  
372 random effect. Significant results ( $p < 0.05$ ) are in bold.

373

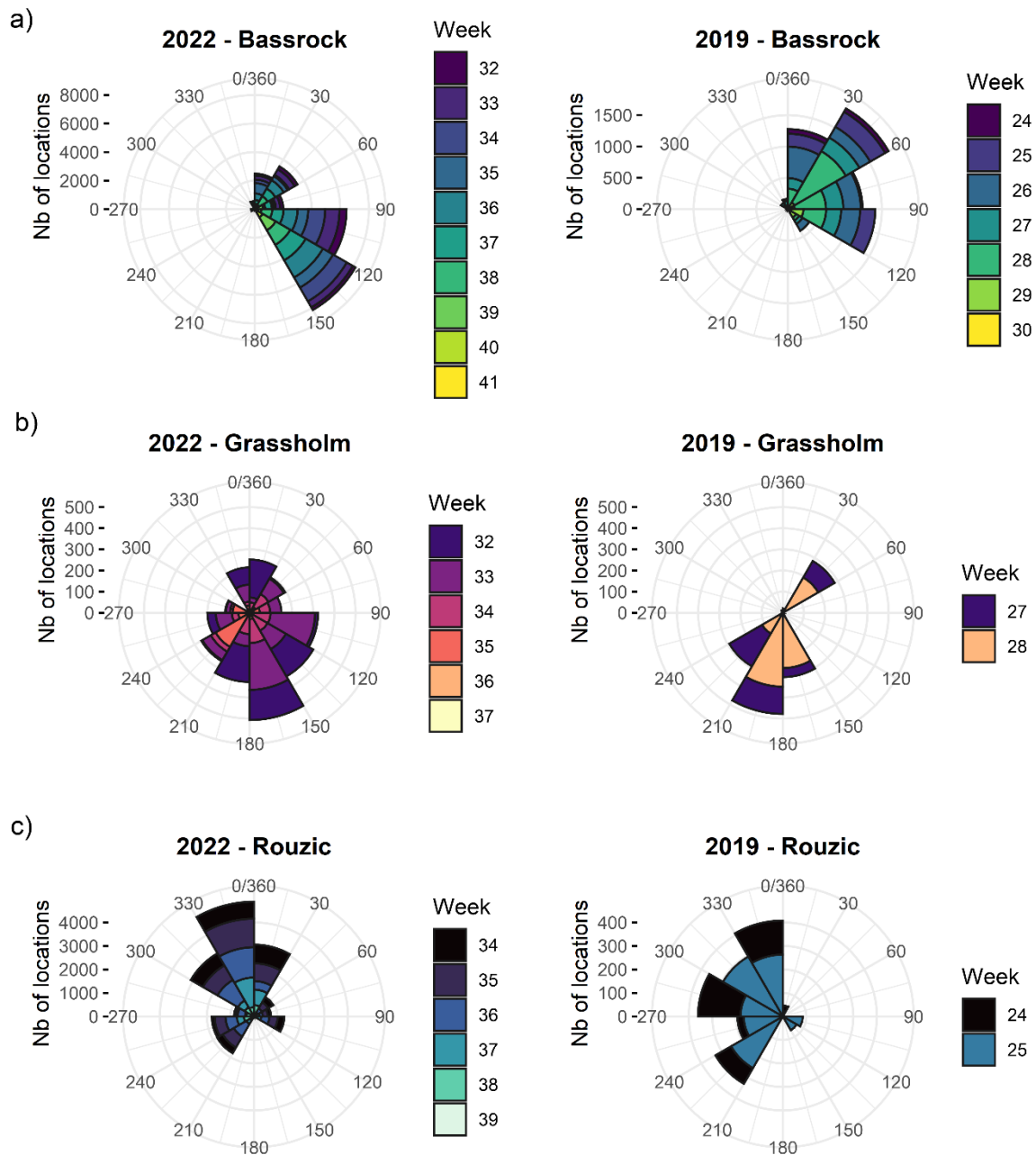
Linear mixed models	Bass Rock				Grassholm				Rouzig			
	Estimate ± SE	df	t-value	p- value	Estimate ± SE	df	t-value	p- value	Estimate ± SE	df	t-value	p-value
<b>Maximal distance</b>	<b>0.009 ± 0.005</b>	<b>299</b>	<b>2.03</b>	<b>0.043</b>	-0.012 ± 0.014	44	-0.85	0.40	-0.003 ± 0.006	243	-0.53	0.60
<b>Total distance travelled</b>	<b>0.011 ± 0.005</b>	<b>299</b>	<b>2.34</b>	<b>0.02</b>	-0.017 ± 0.016	44	-1.07	0.29	1.8e10 <sup>-5</sup> ± 6.0e10 <sup>-3</sup>	243	0.003	0.99
<b>Trip duration</b>	<b>0.013 ± 0.004</b>	<b>299</b>	<b>3.29</b>	<b>0.001</b>	-0.014 ± 0.019	44	-0.74	0.46	0.011 ± 0.006	243	1.73	0.09
<b>Time at the colony between at-sea trips</b>	-0.003 ± 0.003	288	-0.77	0.45	-0.011 ± 0.0010	56	-1.13	0.26	<b>-0.015 ± 0.007</b>	<b>220</b>	<b>-2.09</b>	<b>0.038</b>
Logistic regressions	Bass Rock				Grassholm				Rouzig			
	Estimate ± SE	df	z-value	p- value	Estimate ± SE	df	z-value	p- value	Estimate ± SE	df	z-value	p-value
<b>Proportion of a trip spent resting</b>	0.0053 ± 0.0086	307	0.63	0.53	-0.05 ± 0.05	47	-1.18	0.24	0.018 ± 0.014	253	1.24	0.21 384
<b>Proportion of a trip spent foraging</b>	-0.0017 ± 0.007	307	-0.24	0.81	0.037 ± 0.034	47	1.05	0.29	-0.014 ± 0.015	254	-0.91	0.36
<b>Proportion of a trip spent flying</b>	-0.0028 ± 0.008	307	-0.33	0.74	-0.0021 ± 0.040	47	-0.05	0.96	-0.008 ± 0.018	254	-0.43	0.67 387

388



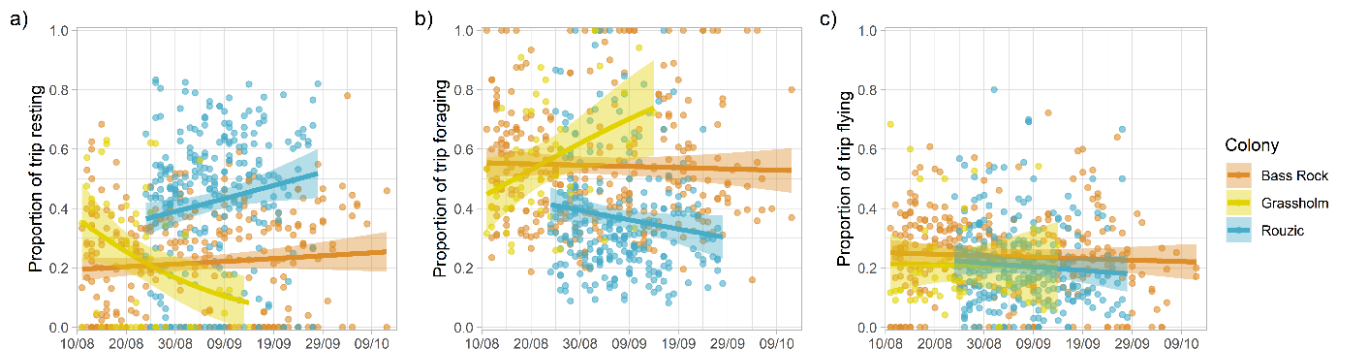
390

391 **Figure 1.** Tracks of gannets nesting in 2022 (left) and 2019 (right) on (a) Bass Rock, Scotland,  
 392 (b) Grassholm, Wales and (c) Rouzic, Brittany, (yellow diamonds). Orange circles represent  
 393 neighbouring gannet colonies to the respective study colonies. Gradual changes in colour  
 394 represent time in days since start of GPS tracking.



395

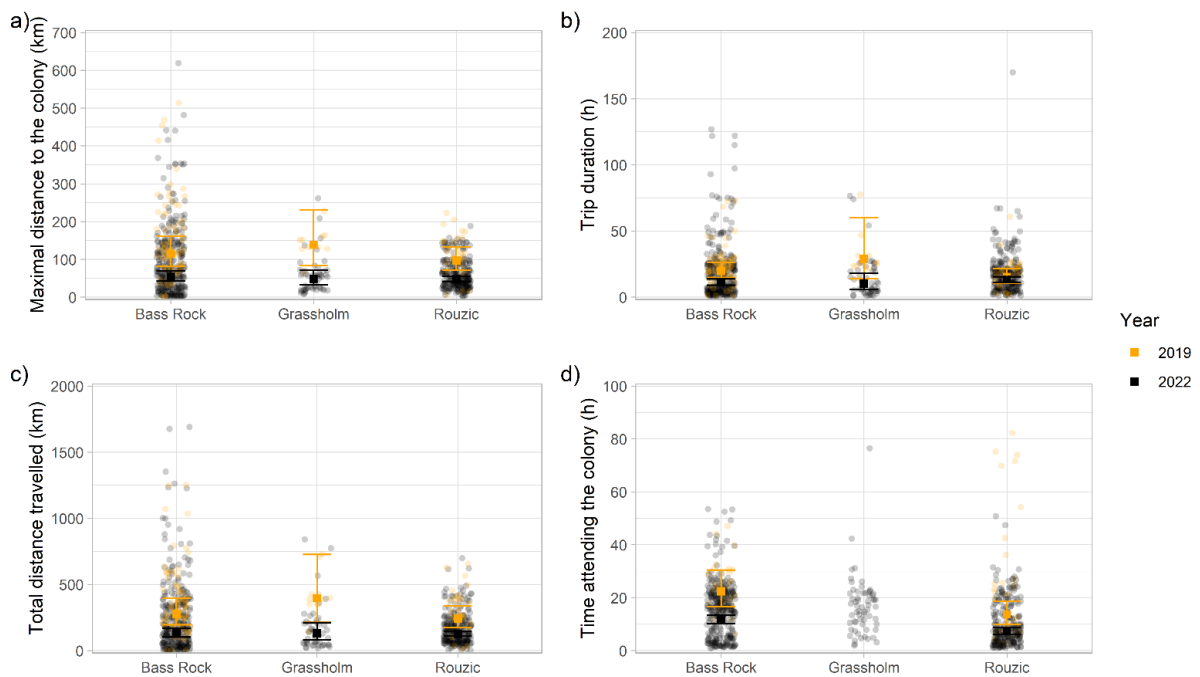
396 **Figure 2.** Rose diagrams illustrating the bearings in 30 degree bins of at-sea locations relative  
 397 to the nesting colony of gannets nesting in 2022 (left) and 2019 (right) on (a) Bass Rock,  
 398 Scotland, (b) Grassholm, Wales and (c) Rouzic, Brittany. The centre of each rose diagram  
 399 represents the colony location, the length of each wedge represents the number of locations  
 400 recorded in that direction over time, in coloured weekly bins.



401

402 **Figure 3.** Proportion of inferred behavioural states [(a) resting, (b) foraging, (c) flying] during  
 403 at-sea trips of gannets nesting on Bass Rock (orange), Grassholm (yellow) and Rouzic (cyan),  
 404 according to dates from August to October 2022. The dots represent raw data and the line  
 405 and shadow, predicted average slope  $\pm$  95% confidence interval.

406



407

408 **Figure 4.** Predicted means  $\pm$  95% confidence interval of trip characteristics and nest  
 409 attendance of gannets nesting on Bass Rock, Grassholm and Rouzic in 2022 (black) and 2019  
 410 (orange). Note that nest attendance values were unavailable for Grassholm in 2019.

411

412

## 413 Discussion

### 414 - Epidemiology

415 Our analyses confirmed that gannets contracted HPAIV, and other investigations also pointed  
416 to HPAIV as the cause of 2022 seabird mass mortalities in western Europe (Falchieri et al.,  
417 2022; Lane et al., 2023). More specifically, we identified H5N1 (clade 2.3.4.4b) in Rouzic birds.  
418 This contrasts with recent HPAIV outbreaks in southern African seabirds (Molini et al., 2020),  
419 which were caused by H5N8 (clade 2.3.4.4b). Our study adds to the evidence that HPAIV has  
420 become established in seabirds, and will probably recurrently re-emerge, as observed in  
421 southern Africa (Molini et al., 2020). We also found that some juvenile gannets had H5N1  
422 antibodies, but no live virus (Suppl. 2). This is in line with recent investigations (Caliendo et al.,  
423 2022) suggesting that birds that survived HPAIV develop an immune response, which could  
424 protect against future infections. Further longitudinal monitoring will nonetheless be  
425 necessary to fully test this hypothesis. Those studies will also clarify the factors leading to intra  
426 and interspecific heterogeneity in avian responses to HPAIV (Keawcharoen et al., 2008), which  
427 are key to our understanding of the potential role of different species as HPAIV maintenance  
428 host or spreaders (Huang et al., 2019).

429 Only one of the 15 birds equipped with GPS on Rouzic tested HPAIV positive using swab  
430 samples (Suppl. 2), and gannets fitted with GPS on Bass Rock and Grassholm could not be  
431 tested. Thus, the epidemiological status of most tracked gannets was not known. Ideally, swab  
432 and plasma samples should have been collected in all birds. Yet, even in the presence of both  
433 sample types, some uncertainty would remain. Notably, a positive plasma sample could reflect  
434 a former, rather than an ongoing infection, and such samples are not adequate to infer  
435 whether a bird is a HPAIV carrier and potential spreader at the time of the blood sample  
436 (Gilbert et al., 2013). Indeed, experimentally infected birds stop excreting the virus after a  
437 week or less (van den Brand et al., 2018). Swab samples are therefore theoretically adequate  
438 during this brief excretion period, but half of those for gannets equipped with GPS on Rouzic  
439 were inconclusive. External wipes were useful indicators of virus circulation in the colony, but  
440 cannot be used with confidence for individual infection status considering the risk of  
441 environmental contamination. Overall, we may therefore conclude that HPAIV was extremely  
442 widespread and circulating at all three gannet colonies given observational data on the degree  
443 of mortality, and that an unknown proportion of GPS-tracked birds could have been

444 symptomatic or asymptomatic carrier of the virus. This knowledge gap clearly calls for further  
445 epidemiological studies during future seabird breeding seasons.

446 - Movement ecology

447 Contrary to our first prediction, we did not detect any change in breeding colony fidelity in the  
448 context of HPAIV outbreaks that started approximately two months previous to data  
449 collection. In contrast to the study performed by Jeglinski and colleagues (2023) during the  
450 initial HPAIV outbreak, none of the gannets we tracked came ashore outside of their  
451 respective breeding colonies while alive. We also found that GPS-tracked gannets did not  
452 significantly modify their foraging patterns across the study period (Table 2; Fig. 1-4). Since  
453 our visits to gannet breeding colonies were extremely limited due to the restrictions in place,  
454 we could not monitor the survival of the chicks of the GPS-tracked gannets. Some birds may  
455 have lost their chicks during the study period. Yet, all tracked birds continued to regularly  
456 commute between at-sea feeding sites and their respective colonies, and none of them rested  
457 on the mainland or on other islands in-between trips.

458 Further, gannet foraging effort seemed lower than during the 2019 breeding season (hence  
459 before HPAIV) at our three study sites (Grémillet et al., 2006; Hamer et al., 2007; Patrick et al.,  
460 2014) (Fig. 1, 2 and 4, Table S3). Therefore, in accordance with our second prediction, gannets  
461 surviving HPAIV may have benefited from reduced food competition following the death of  
462 adults and chicks. Nevertheless, these results have to be taken with caution since, as  
463 mentioned in the methods section, the 2022 GPS tracking sessions occurred during late chick-  
464 rearing, whereas the 2019 tracking data were collected during early chick-rearing.

465 Our results are coherent with high breeding and foraging site fidelity in colonial seabirds  
466 (Danckwerts et al., 2021), and contrary to the idea that gannets that have witnessed and  
467 survived mass mortality at their breeding colony modify their movement patterns as a  
468 consequence of the disease outbreak and maintain these changes several months after the  
469 event. Thus, it appears that longer-term enhanced HPAIV transmission throughout the  
470 metapopulation and potentially throughout the co-existing seabird populations is unlikely for  
471 adult breeding gannets. This is an essential piece of information that contributes to a better  
472 understanding of HPAIV transmission dynamics, since wild birds carrying HPAIV are



473 recurrently presented as virus spreaders to farm poultry (Global Consortium for H5N8 and  
474 Related Influenza Viruses, 2016).

475 However, the data we presented here are collected following the initial disease outbreak to  
476 study long-term behavioural responses, and they are only representative of the adult breeding  
477 age class. Other age classes may differ in their propensity to act as a vector for HPAIV. Notably,  
478 immature gannets have been shown to perform visits to other breeding colonies throughout  
479 the breeding season (Votier et al., 2011) and thus likely regularly move between colonies.  
480 These prospecting movements would appear to require limited time/energy investment: For  
481 gannets from Bass Rock, the closest alternative colony is Troup Head on the Scottish mainland  
482 (ca. 210 km), for Grassholm it is Great Saltee in Ireland (ca. 90 km), and for Rouzic it is Ortac  
483 in the British Channel Islands (ca. 130 km) (Fig.1). Reaching these neighbouring colonies would  
484 take 3.2 hrs (Bass Rock), 1.4 hrs (Grassholm), or 2 hrs (Rouzic), assuming a  $65 \text{ km}\cdot\text{h}^{-1}$  travelling  
485 speed (Grémillet et al., 2004). Forthcoming studies will clarify the respective potential of  
486 juvenile and immature gannets to act as vectors in HPAIV transmission. Also, even if rated as  
487 rare (Boulinier et al., 2016), at-sea HPAIV transmission may occur within, and between seabird  
488 species. This might be facilitated by aggregations at natural foraging sites or whilst feeding on  
489 fishery wastes behind trawlers, or through kleptoparasitism and scavenging (Wille et al.,  
490 2016). Studying interspecific fine scale space-use overlap at sea is therefore a high priority for  
491 future monitoring and evaluation of disease transmission scenarios (Boulinier, 2023).

492

#### 493 - Outlook

494 It remains unclear how gannets contracted HPAIV, since they were either at sea, or at their  
495 breeding colony during the outbreak. Larids (*Larus sp.*) or great skuas that klepto-parasitise  
496 gannets might be potential vectors since they use similar terrestrial and marine habitats  
497 (Falchieri et al., 2022), but further analyses will be necessary to test these hypotheses. HPAIV  
498 first affected gannets in Iceland, Québec and Scotland (from early April 2022), and  
499 subsequently arrived in Brittany (from early July 2022)(Lane et al., 2023). Hence, it is possible  
500 that immature gannets moving between these colonies may have spread the virus, but this  
501 pathway is still hypothetical. Equally unknown are HPAIV dynamics during gannet migration,  
502 which started in September-October 2022. These inter-breeding movements took gannets

503 from the British Isles and Brittany to the Mediterranean or West Africa (Fort et al., 2012). Off  
504 Africa, gannets met with some of their North American conspecifics, as well as with a vast  
505 community of North Atlantic seabirds spending the winter in tropical waters (Grecian et al.,  
506 2016). In February 2023, surviving gannets returned from migration and started breeding  
507 again. Further investigations are now required, notably to clarify HPAIV impacts on gannet  
508 movement ecology and population dynamics across age classes, and multiple years.

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

520

521 Author contributions: DG, PP and SCV designed the study, with advice from SW and JJ. DG, PP,  
522 APr, TP, JJ, SCV, JM, AB, JF, NC, RJ, LL, AT, NS and JL were leading the field studies including  
523 funding acquisition, permit acquisition and field data collection. APo, PP, MA-Z, AG, NC and  
524 DG analysed the data. DG, APo, AG and JJ wrote the paper, with inputs from all other authors.

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536 Gamble was supported by the Royal Society through a Newton International Fellowship.

537 Ethics: All procedures followed the *guidelines for the treatment of animals in behavioural*  
538 *research and teaching* of the *Association for the Study of Animal Behaviour*. Bass Rock:  
539 fieldwork was performed in partnership with the Scottish Seabird Centre with permission of  
540 the landowner of the Bass Rock, Sir Hew Dalrymple, and under a special method endorsement  
541 and ringing permit of the British Trust for Ornithology BTO to Jana Jeglinski. Colour ringing was  
542 performed under a permit to Jude Lane from the BTO. We conducted our fieldwork under an  
543 exemption to the general ringing ban in seabird colonies granted by NatureScot which  
544 permitted us to capture and tag gannets during the HPAIV outbreak. All fieldwork was  
545 performed with the required risks assessments and ethical approval in place. Grassholm: All  
546 research was carried out under licence (RSPB, Natural Resources Wales (#S091127-1), British  
547 Trust for Ornithology (BTO: A4257), the BTO Special Methods Panel and the UK Home Office  
548 (30/3065). Rouzic: fieldwork operated under the Programme Personnel de baguage n°536  
549 CRBPO/MNHN validation 2020-2024.

550

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

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