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No impact of black-eye symptom on foraging behaviour and reproductive success of Northern gannets following highly pathogenic avian influenza

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ABSTRACT

Highly Pathogenic Avian Influenza Virus (HPAIV) is currently causing major wild animal population crashes all over the world including Antarctica. Yet, there are important knowledge gaps on the implications of long-lasting symptoms for the ecology of surviving individuals and the conservation of their populations. Using GPS tracking devices and long-term demographic data, we examined the effects of HPAIV on a seabird population of Northern gannets (*Morus bassanus*) in the colony of Rouzic, France. One year after the HPAIV outbreak of 2022, the breeding gannet population declined by 38 % and 22.3 % of surviving breeders were zombie birds: they had darkened irises, a black-eye symptom indicative of past infection to HPAIV. Importantly, we demonstrate that black eyes were not associated with detectable differences in the foraging behaviour and habitat use of surviving breeding gannets. Compared to years prior to the outbreak, the foraging effort of breeding individuals was lower and breeding success was higher, aligning with Ashmole's halo hypothesis, which posits that smaller seabird populations face lower intra-specific competition for food in the vicinity of their breeding colony and thereby, have a reduced foraging range. Our results highlight the importance of density-dependant mechanisms in population responses to sudden mass-mortalities, but raise conservation concerns, especially for species facing cumulative threats. In the long-term, locally depleted populations may reach critical thresholds where individual abundance and productivity may not be sufficient to maintain a positive demographic growth rate, ultimately leading to local population extinctions.

1. Introduction

Infectious diseases represent a major threat to biodiversity (Smith et al., 2006) but may have contrasting impacts on host population dynamics. At the population level, high mortality rates during episodic outbreaks often cause dramatic population declines and may put species at risk of extinction (Smith et al., 2009; Smith et al., 2006). Yet, sudden reductions in local population sizes due to high mortality rates may also relax density-dependent limiting factors such as intra-specific competition for access to reproduction. This may notably result in higher local recruitment rates: more immatures recruit at an earlier age and compensates for the disappearance of older breeding competitors (Crespin

et al., 2006; Katzenberger et al., 2021; Votier et al., 2008). At the individual level, infectious diseases may either favour or hinder host movements (Dougherty et al., 2018). On one side, infectious diseases may directly reduce the locomotor activity of the infected individuals and limit their ability to move through the landscape, thereby reducing population connectivity (Binning et al., 2017; Duriez et al., 2023; van Gils et al., 2007). On the other side, non-infected individuals may actively respond to disease outbreaks by changing their behaviour and moving more and/or further (Careen et al., 2024; Genton et al., 2015; Jeglinski et al., 2024b; Ponchon et al., 2024). Therefore, investigating the effects of infectious diseases on both individual behaviour and demography is essential for predicting their short and long-term

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consequences on host population trajectory and persistence. Such knowledge is key to conservation planning but difficult to acquire in wild species (Herrera and Nunn, 2019).

Seabirds are one of the most threatened bird groups (Grémillet et al., 2018; Phillips et al., 2023). At sea, they suffer from incidental bycatch and competition for food resources with fisheries, changes in food distribution and abundance due to global warming, and pollution. On land, they suffer from breeding habitat loss and predation by alien invasive species. As a result, the world seabird populations have declined by half since 1970 (Grémillet et al., 2018). Even if diseases have not been a major concern for seabird populations so far (Dias et al., 2019), they can have a significant impact and may lead populations to extinction (Smith et al., 2006). In this context, the emergence and worldwide rapid spread of new emerging infectious diseases may jeopardize ongoing conservation efforts. Avian Influenza (AIV), commonly known as bird flu, is a contagious viral disease. The virus can be transmitted through aerosols, large droplets, or direct contact with secretions (Tellier, 2006) and primarily affect domestic and wild birds (Alexander and Brown, 2009). In 2020, a particularly deadly lineage of Highly Pathogenic Avian Influenza virus (HPAIV), clade H5N1 2.3.4.4b, emerged in the Northern hemisphere, causing the death of millions of farmed poultry as well as millions of wild terrestrial and marine birds and mammals (Falchieri et al., 2022; Wille and Barr, 2022). It has since then spread to all continents except Oceania and has become a concerning zoonotic (Peacock et al., 2025).

Northern gannets *Morus bassanus* are long-lived seabirds which are highly faithful to their breeding colony and foraging areas (Wakefield et al., 2015). They were among the first seabird species massively hit by HPAIV in 2022, with high mortalities of both adults and chicks across their breeding range (Careen et al., 2024; Grémillet et al., 2023; Lane et al., 2024). They were also the only seabird species where epidemiological and tracking data were collected to examine the immediate impacts of HPAIV on their spatial behaviour. At the worse of the HPAIV outbreak, two studies carried out in Bass Rock, UK (Jeglinski et al., 2024a) and Cape St. Mary's, Newfoundland, Canada (Careen et al., 2024), highlighted a change in foraging patterns of surviving adult gannets, which performed longer trips in distance and duration, sometimes associated with prospecting visits to other colonies, specific movements never documented in adult gannets before. Furthermore, 78 % of individuals presenting high levels of H5 antibodies, indicator of a previous HPAIV infection, had unusual dark or spotted irises but all tested negative to HPAIV at the time of sampling. This black-eye symptom was suggested to indicate that those birds had been infected by HPAIV in the previous weeks/months and kept an external sign of infection through a modification of their iris colour (Lane et al., 2024). At the end of the outbreak, in August 2022, a complementary study combining tracking data from 3 major European gannet colonies, including Bass Rock, demonstrated that surviving adults remained faithful to their breeding sites and foraging habits, and that foraging effort was lower than years prior to the outbreak (Grémillet et al., 2023). It was nevertheless unclear whether the black-eye symptom would remain the following year and whether it would affect the foraging behaviour of breeding adults.

Here, we performed the first longer-term evaluation of the incidence of HPAIV on the foraging behaviour and reproductive success of Northern gannets one year after the catastrophic outbreak of 2022. During the 2023 breeding season, we examined whether the foraging behaviour of adult gannets breeding in the colony of Rouzic (France), was altered due to their iris colour. Indeed, change in iris colour from pale blue/grey to dark has been shown to be an external sign of previous exposure to HPAIV but potential consequences on individual behaviour remain untested (Lane et al., 2024). Irises are circular areas which constrict or dilate pupils and controls the amount of light reaching the retina in the back of eyes. Their colour, made of different pigments and structures, also absorbs or reflects light (Corbett et al., 2024). We therefore hypothesized that a modification of iris colour would alter

individual visual clarity and thus, tracked birds with at least one spotted or dark iris would display different at-sea behaviours or habitat use compared to birds with normal irises. We also accounted for sex, as female gannets generally have a higher foraging effort during the breeding season compared to males (Clark et al., 2021; Cleasby et al., 2015; Lewis and Benvenuti, 2002; Stauss et al., 2012). Second, we used long-term annual tracking data collected between 2005 and 2023, to test the hypothesis that the outbreak reshaped the gannets' foraging behaviour due to demographic readjustments and potential density-dependent effects. Indeed, the Ashmole's halo hypothesis posits that seabird populations are regulated by food supply in the immediate vicinity of their breeding colonies, with their foraging activity leading to prey depletion 'halos' around the colonies (Ashmole, 1963). As a result, larger seabird colonies tend to have larger foraging range due to higher intra-specific competition (Patterson et al., 2022). The HPAIV outbreak in 2022 killed an estimated 54 % of adult gannets and substantially reduced intra-specific competition for food (Grémillet et al., 2023). We therefore predicted a significant decrease in foraging effort and a higher breeding success at the population level in 2023, compared to pre-outbreak levels.

2. Material and methods

2.1. GPS tracking in 2023

The study was carried out at the gannet colony of Rouzic, Brittany (48°54'N, 3°26'W), the southernmost colony in Europe. In total, 26 breeding adults (12 females and 14 males) rearing chicks aged 2–8 weeks were tracked with GPS-GSM OrniTrack-9 tags (Ornitela, solar powered, mass 9 g, 0.3 % of bird body mass, dimensions 37 × 19 × 12 mm, plus ~10 cm external whip antenna) from July 2, 2023 to October 17, 2023, before the tags naturally fell off with tail feather moult (Table 1). All birds were caught at the nest with a noose mounted on a telescopic pole and handled in the shade away from the colony within 10 min. Their head was covered with a sheet to minimize stress and we favoured early morning and late afternoon cooler hours. Birds were specifically selected to balance the number of individuals with at least one dark or spotted iris or two pale irises. During handling and using biosecurity equipment, birds were fitted with a metal and plastic ring with a unique alphanumeric combination. All equipped birds had the iris colour of their eyes inspected and photographed by the same team. Irises were classified as normal (pale iris with no, or < 3 small dark spots; Fig. 1a), spotted (pale iris and > 3 larger dark spots; Fig. 1b) or dark (completely black iris; Fig. 1c). In detail, 2 individuals had 2 dark irises, 6 individuals had 1 dark and 1 pale irises, 1 individual had 1 dark and 1 spotted irises, 2 individuals had 2 spotted irises and 2 individuals had 1

Table 1

Details of the GPS tracking dataset and trip characteristics of gannets breeding on Rouzic in 2023 depending on their iris colour. Results are expressed as mean ± standard error (min-max).

| | Zombie birds with at least one spotted/dark iris | Normal birds with two pale irises |
|--|--|-----------------------------------|
| Nb of tracked birds | 13 | 13 |
| Tracking period | 04/07–18/10 | 05/07–14/10 |
| Total number of foraging trips | 494 | 485 |
| Mean number of foraging trips per individual | 38.0 ± 5.0 (7–75) | 37.3 ± 3.9 (13–56) |
| Mean tracking duration per individual (days) | 48.7 ± 4.6 (13.6–74.0) | 56.8 ± 4.77 (26.5–83.7) |
| Mean maximal distance to the colony (km) | 76.3 ± 6.2 (44.4–121.4) | 88.1 ± 6.1 (60.6–132.1) |
| Mean maximal distance travelled (km) | 213.5 ± 18.1 (112.3–349.0) | 247.2 ± 20.0 (150.0–400.6) |
| Mean trip duration (h) | 17.9 ± 1.8 (7.8–30.3) | 21.6 ± 1.8 (11.1–31.1) |
| Mean nest attendance (h) | 15.8 ± 0.7 | 16.4 ± 1.1 |

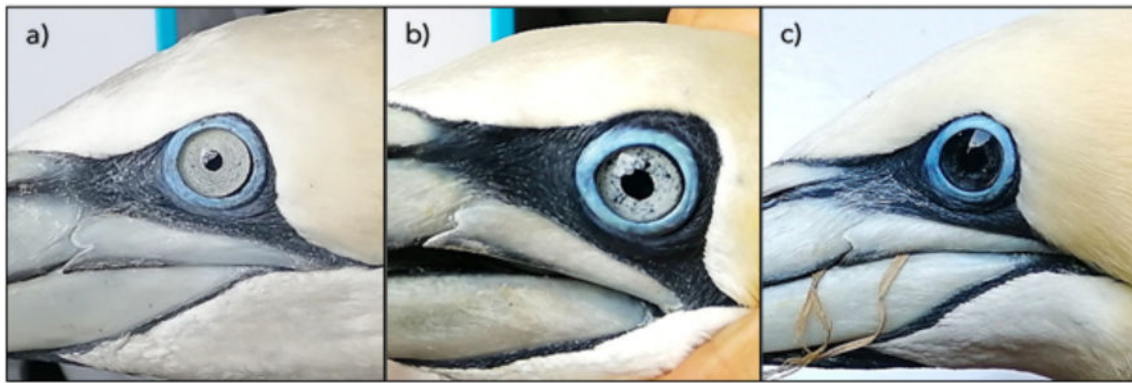


Fig. 1. Picture of iris colour in a gannet with normal pale iris (a), spotted iris (b), dark iris (c).

spotted and 1 pale irises.

Blood samples were taken from the tarsal vein for serological analysis. They revealed that 100 % of the birds with at least one spotted or dark iris were seropositive for anti-AIV NP and anti-AIV H5 (Boulinier et al. unpublished). Only one bird with 2 pale irises was seropositive. Accordingly, we divided the equipped birds in two groups: the 'normal' birds with two pale irises ($n = 13$; Fig. 1a) and the 'zombie' birds, with at least one spotted or dark iris ($n = 13$; Fig. 1b-c).

Tags were attached with Tesa® tape to the three central tail feathers. Once released, most birds returned immediately to their nests, at the latest within 1 h. GPS-GSM tags were pre-programmed to send data to a server using mobile-phone network so that data were transmitted from anywhere within 2G coverage and accessed by the user in near-real-time. All tags recorded a GPS position every 10 to 60 min, depending on battery voltage. Tracks from 2023 were compared with GPS tracking data gathered for gannets of the same colony across 12 years since 2005 (see Table S1 for sample sizes and Grémillet et al., 2023; Le Bot et al., 2019 for tracking methodology).

2.2. GPS data processing

Data were analysed using R 4.2.0 (R Core Team, 2022). Tracking data from 2022 and 2023 were imported from Movebank data repository using the R package *move* (Kranstauber et al., 2023). Tracking data from previous years (2005–2006; 2010–2017; 2019) were imported from csv files. For all years, foraging trips were defined as periods when birds were > 1 km away from the colony for > 1 h. Trips in 2023 with time gaps longer than 6 h and incomplete trips were excluded. Data from other years did not have gaps.

Because some tracks in 2023 had irregular sampling, data were linearly interpolated when there was less than 30 min between two successive points and adjusted to the closest 10 min. Time gaps longer than 30 min were not interpolated. The 2023 at-sea distribution was estimated with the utilization distribution (UD) of the tracked birds on a 500 m resolution grid covering the English Channel, using the biased random bridge method (BRB; Benhamou, 2011) to account for autocorrelation in GPS locations. Overlaps between 90 % UD of zombie and normal birds, as well as between males and females in 2023, were determined by the Bhattacharyya's affinity index (Fieberg and Kochanny, 2005), which ranges from 0 (complete spatial segregation) to 1 (complete overlap). Each individual at-sea trip (2023 and historic data) was characterized by its maximal distance to the colony, total trip duration and total distance travelled. Nest attendance was estimated in 2023 only using the time spent in the colony between two consecutive at-sea trips. Those 4 parameters, which are proxies for the at-sea foraging effort of seabirds, were used as response variables.

2.3. Statistical analyses

To explore potential associations between gannet movements, nest attendance and black-eye symptom, a first set of linear mixed models (LMM) were fitted with the *nlme* package (Pinheiro and Bates, 2023) on square-root transformed trip characteristics and nest attendance for 2023, with iris colour, sex and their two-way interactions as well as day of the year (day 150 = 29 May; day 300 = 26 October), as fixed effects. Note that preliminary LMM did not detect significant and consistent differences ($p > 0.03$) in the at-sea behaviour among individuals with different degrees of altered irises (1 or 2 spotted/dark irises; $n = 13$). This is why all affected birds were pooled in one category (zombie birds).

A second set of LMM were fitted on square-root-transformed trip characteristics with year as a fixed effect to determine whether foraging effort significantly differed between years. 2005, first year of the tracking period, was selected as the reference year, when colony size was the lowest before the outbreak. Sex was not included in the inter-annual analysis due to missing data. In all LMM, bird ID was included as a random effect to account for multiple measures from the same individual. Model assumptions were checked with the *DHARMa* R package (Hartig, 2021).

2.4. Demographic survey

A long-term monitoring survey has been carried out since the 1960s at Rouzic. Every year, the colony size is estimated from direct counts of apparently occupied nests on aerial photos taken during incubation, between mid-May and early June. Breeding success was monitored from 2013 onward, based on a sample of 100 apparently occupied nests, followed from April through September, using a remotely controlled camera permanently installed at 2 m on a pole in the core of the colony. The camera can scan hundreds of nests thanks to a rotating system and a powerful zoom. Here, annual breeding success is defined as the average number of fledglings (between 0 and 1) produced per active nest. The proportion of zombie birds (at least one spotted or dark iris) among all breeders was estimated using the camera zoom based on a random number of nests situated in the camera field.

3. Results

3.1. Foraging behaviour of gannets in 2023, one year after HPAIV outbreak

All 26 GPS tags deployed in 2023 provided between 7 and 75 individual foraging trips for a duration of 13 to 84 days (Table 1). No sign of active HPAIV was detected in the colony in 2023 but 22.3 % of breeding gannets were zombie birds: they had at least one spotted or dark eye. Changes in iris colouration, reflecting a previous exposure to AIV, did

not affect at-sea movement patterns of Northern gannets: the 13 zombie birds exhibited statistically similar maximal distance ($F_{1,22} = 1.83$; $p = 0.19$), total distance ($F_{1,22} = 1.24$; $p = 0.28$) and trip duration ($F_{1,22} = 1.63$; $p = 0.22$), compared to the 13 normal individuals (Table 1). Both groups used the same foraging areas (Fig. 2a), indicated by a high Bhattacharyya's affinity index value (0.86). The effect of the interaction between sex and iris colour on trip characteristics was not significant ($p > 0.28$ for all 4 response variables) but sex alone was significant. Females undertook longer trips than males (females: $n = 12$; $23.5 \text{ h} \pm 1.7$ vs. males: $n = 14$; $16.6 \text{ h} \pm 1.4$; $F_{1,22} = 11.51$; $p = 0.003$), and travelled further both in terms of maximal distance (females: $94.8 \text{ km} \pm 6.9$ vs. males: $71.4 \text{ km} \pm 4.0$; $F_{1,22} = 9.30$; $p = 0.006$) and total distance travelled (females: $282.7 \text{ km} \pm 20.5$ vs. males $194.0 \text{ km} \pm 11.8$; $F_{1,22} = 12.31$; $p = 0.002$). Yet, males ($n = 14$) and females ($n = 12$) shared the same foraging areas (Bhattacharyya's affinity index = 0.91; Fig. 2b). All trip characteristics significantly increased throughout the chick-rearing season (Fig. 3a-c). Nest attendance between two at-sea consecutive trips was similar between normal and zombie birds ($F_{1,22} = 0.54$; $p = 0.47$; Table 1) and between sexes ($F_{1,22} = 2.01$; $p = 0.17$) but significantly increased throughout the season ($F_{1,944} = 4.57$; $p = 0.03$; Fig. 3d).

3.2. Inter-annual variation of foraging behaviour, breeding success and colony size (2005–2023)

In 2023, the gannet colony of Rouzic suffered a 38 % size decline, going from an estimated 18,747 active occupied nests before the HPAIV outbreak in 2022, to 11,592 active occupied nests in 2023 (Fig. 4a). Individual breeding success rebounded from 0.03 fledgling produced per active nest in 2022 to 0.58 in 2023, higher than the long-term average of 0.48 (Fig. 4a). Gannet foraging effort varied substantially across 2005–2023, along with annual colony size and breeding success (Fig. 4b-d). Foraging trips in 2022 and 2023 were significantly shorter in terms of range ($F_{1,12} = 6.63$; $p < 0.001$), total distance ($F_{1,12} = 11.1$; $p < 0.001$) and duration ($F_{1,12} = 2.47$; $p = 0.005$), suggesting a lower foraging effort in the two most recent years. On the contrary, foraging

trip duration was longest in 2014 and 2015, when colony size was at its largest ($p < 0.02$; Fig. 4). Trip duration, maximal distance and total distance travelled all significantly increased with colony size ($p < 0.005$; Fig. 5a-c). Within each year, all trip characteristics significantly increased throughout the breeding season (Fig. 5d-f).

4. Discussion

In 2022, the global population of Northern gannets was hit by an unprecedented outbreak of HPAIV (Lane et al., 2024). In the European southernmost gannet colony of Rouzic, France, population size decreased by 54 % between the beginning and end of the chick-rearing season (Grémillet et al., 2023) and fledging success was reduced to 0.03 fledgling per pair (Fig. 4a). One year later, in 2023, our study shows that although 22.3 % of breeding gannets presented a long-lasting black-eye symptom caused by HPAI, their at-sea behaviour was not altered compared to individuals with normal eyes. Moreover, even if population size actually declined by 38 % compared to the previous year, fledging success rebounded to 0.58, probably because of a release in density-dependence for the access to food resources.

Contrarily to our expectations, zombie birds with at least one spotted or dark iris used the same foraging areas as normal birds (Fig. 2) and dedicated the same foraging effort to find their food at-sea (Fig. 3). Therefore, past exposure to HPAIV and associated change in iris colour did not affect the foraging behaviour and habitat use of zombie gannets during the next breeding season. This implies that individuals' visual acuity and ability to navigate or find food at sea was not impaired. Likewise, change in iris colour did not prevent zombie birds from surviving HPAIV and breeding the following year. Black-eye symptom therefore appears to be non-lethal and do not require any behavioural readjustment in zombie birds. We confirm that this symptom could be used as a simple proxy to monitor the proportion of individuals that have been exposed and have survived HPAIV, as suggested by Lane et al. (2024).

In addition to individual's visual acuity, iris colour has been

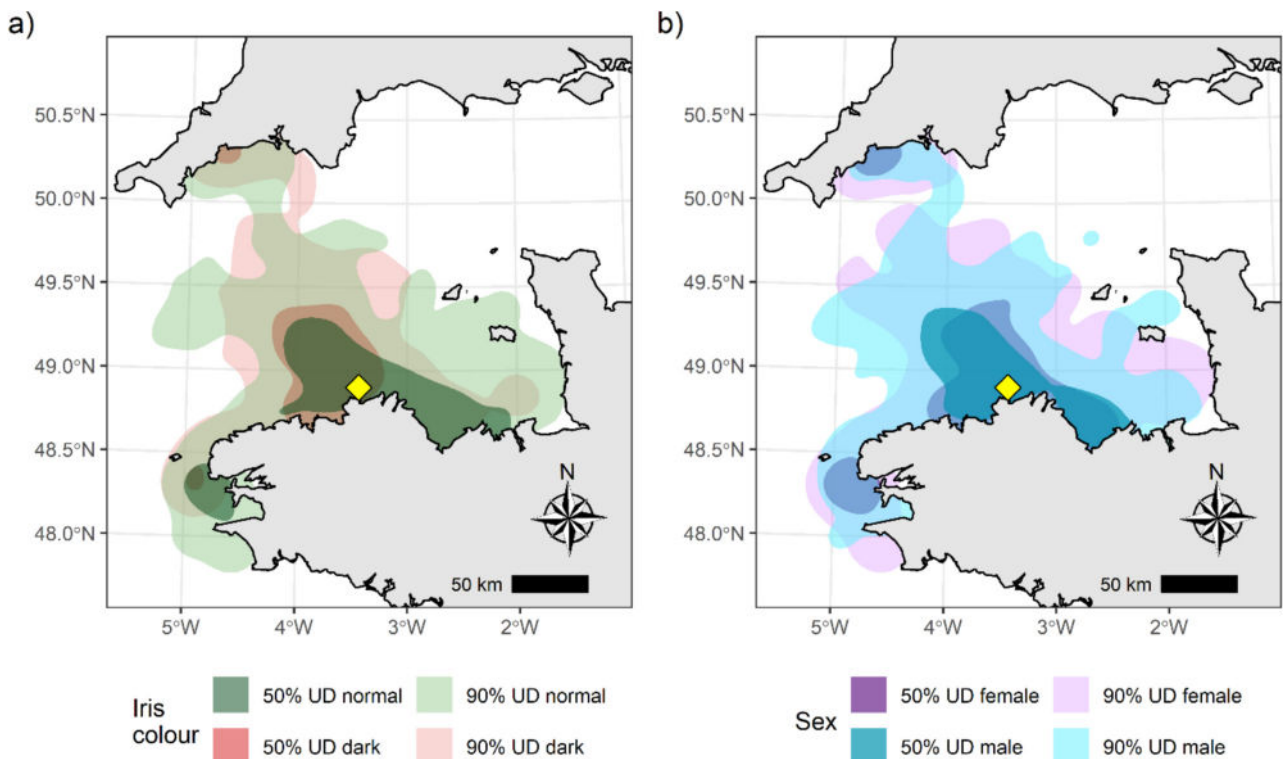


Fig. 2. Utilization distribution of Northern gannets tracked in Rouzic (yellow diamond) in the English Channel during chick-rearing 2023 according to their iris colour (a) and sex (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

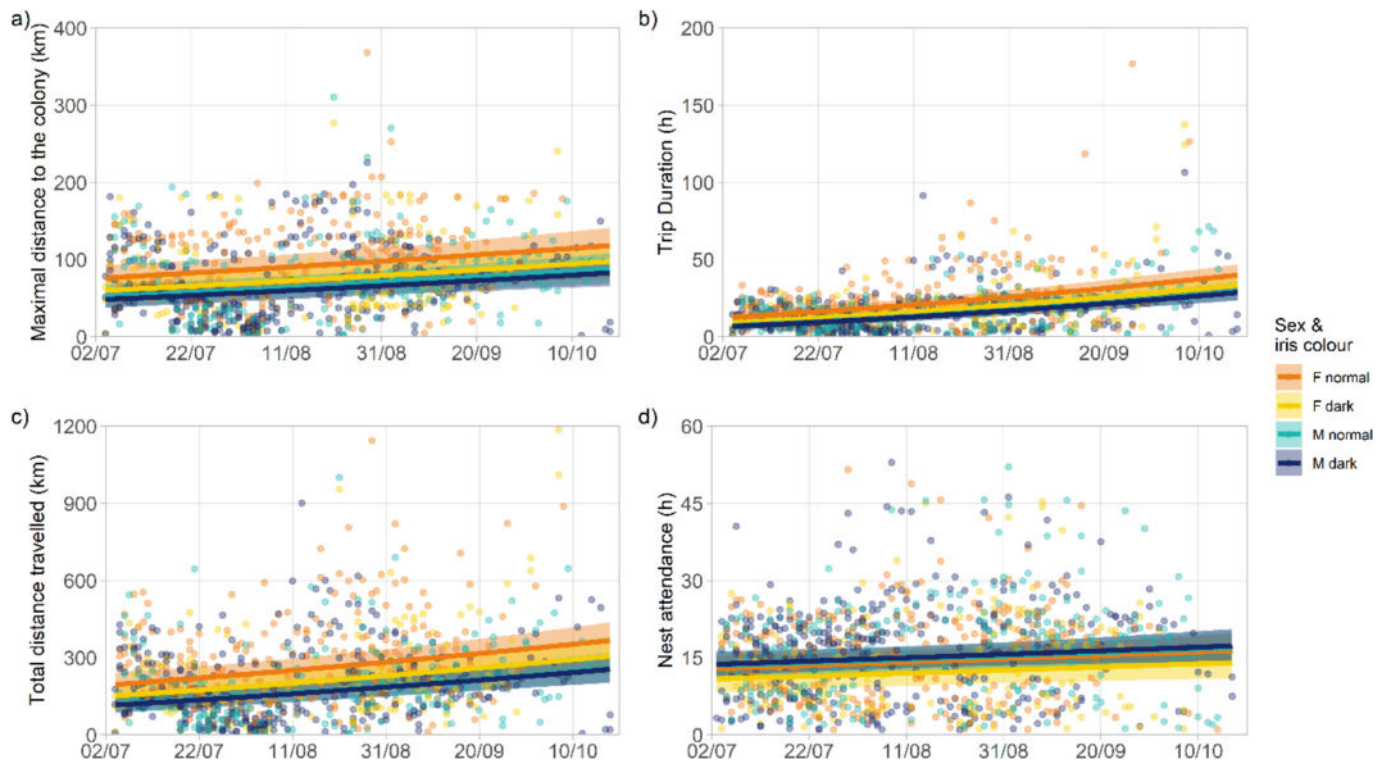


Fig. 3. Trip characteristics and nest attendance of male (M) and female (F) Northern gannets nesting on Rouzic according to their iris colour (dark or normal) from July to October 2023. The dots represent raw data and the line and shadow, the predicted average slope \pm 95 % confidence interval.

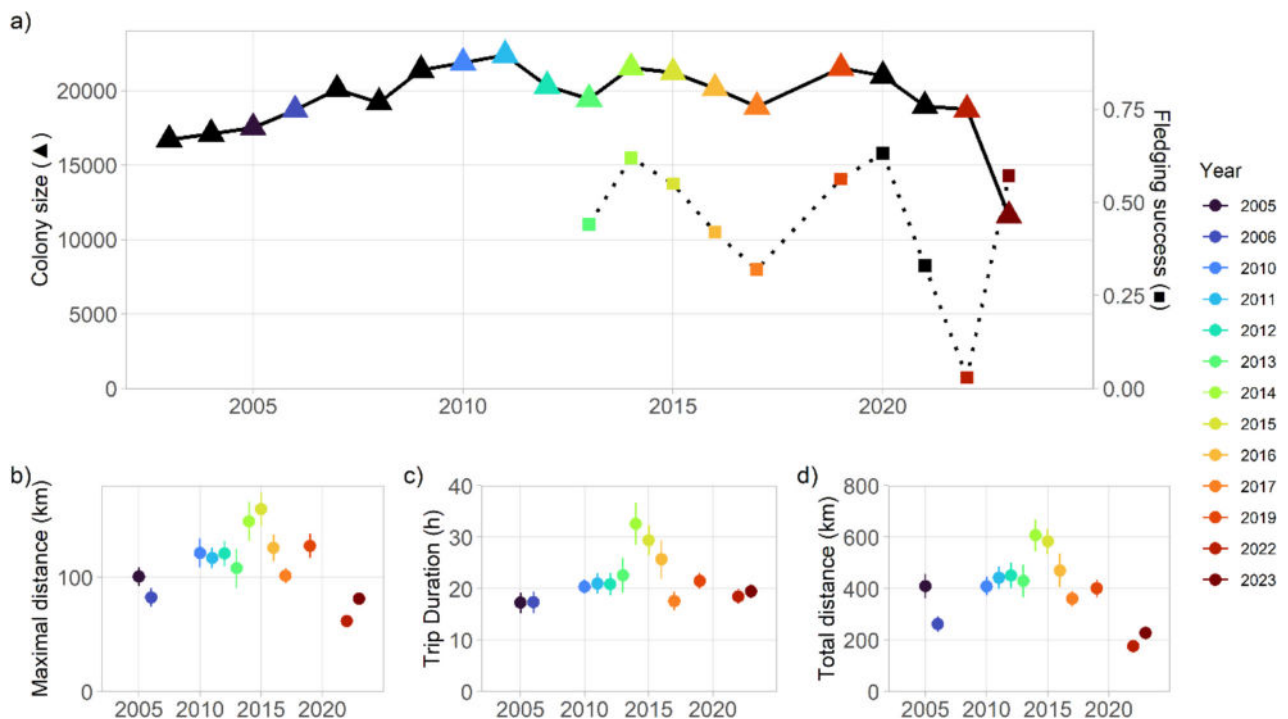


Fig. 4. (a) Temporal dynamics of colony size reflected by the number of active occupied nests (filled triangles) and fledging success (filled squares) of Rouzic. (b) Mean \pm SE maximal distance to the colony (c) Mean \pm SE trip duration (d) Mean \pm SE total distance travelled by gannets during the 13 years of GPS tracking in Rouzic. Colors refer to years with available tracking data.

suggested to play a role in sexual selection in birds (Corbett et al., 2024). If dark iris colour reflected individual long-term survival to HPAIV, it might convey to potential mates a positive signal on individual fitness and might differentially contribute to select for individuals resistant to

HPAIV (Andersson, 1994; Davidson et al., 2017; Thomas et al., 1995). However, we do not know whether the black-eye symptom is associated with a heritable ability to resist to HPAIV and whether it is reversible on the long-term. Further studies need to be conducted to monitor iris

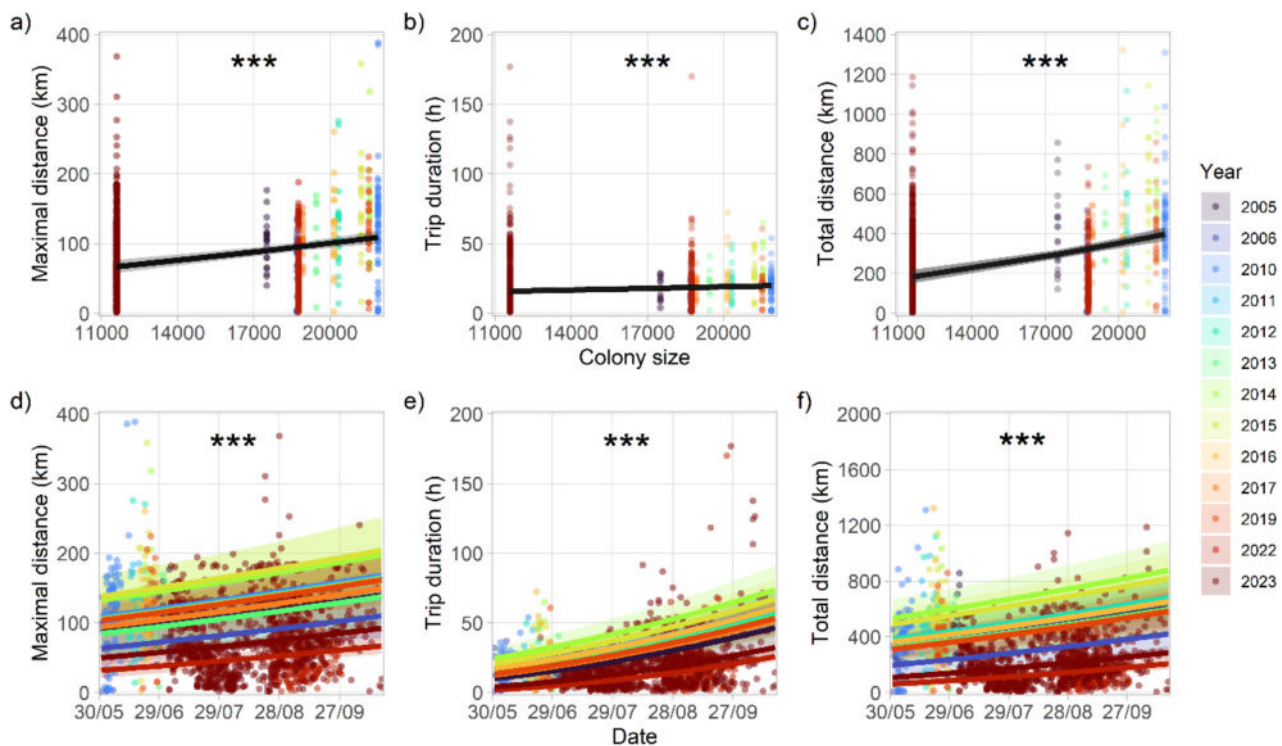


Fig. 5. Predicted relationship from linear mixed models between (a/d) maximal distance to the colony, (b/e) trip duration and (c/f) total distance travelled and the annual colony size of Rouzic (upper panel) and day of the year (lower panel). Colour points represent raw data, the line and shadow, the predicted average slope \pm 95 % confidence interval and *** reports significant relationships (p -values < 0.005).

colour of known birds over several consecutive years along with serological status to HPAIV, to assess whether black eyes actually convey information on individual immunity and impact mating and breeding success.

The only difference we detected in the foraging effort among individuals in 2023 was due to sex. Females performed longer trips in distance and time compared to males, but still shared the same foraging areas (Figs. 2, 3). This difference in foraging effort has already been reported in other gannet colonies (Clark et al., 2021; Cleasby et al., 2015; Lewis and Benvenuti, 2002; Stauss et al., 2012) and has been explained by unequal energetic demands coupled with a natural resource partitioning due to inter-sexual competition (Bennison et al., 2022).

When comparing more closely the foraging behaviour of all the tracked breeding gannets over the years, trips were significantly shorter in 2022 and 2023 in terms of total distance, range and duration compared to the first year of tracking in 2005, suggesting a lower foraging effort in the two most recent years (Fig. 4). Moreover, foraging effort was positively correlated with annual colony size (Fig. 5). This supports our hypothesis that because of the high mortality event in 2022 and subsequent strong population decline in 2023, density-dependant competition for food resources was alleviated and breeding gannets foraged closer to their colony and for shorter durations. This may have positively impacted their body condition, as their breeding success was one of the highest of the last 10 years (Fig. 4). When intra-specific competition is high and/or when natural food resources such as mackerel are scarce, breeding gannets nesting in Rouzic increase their foraging effort and consume more fishery discards, which alters their body condition and reproductive success (Le Bot et al., 2019). The combination of low foraging effort and high breeding success in the two most recent years therefore further indicates a release of intra-specific competition to access natural food resources, after the HPAIV-induced population crash. Within each year, individual tracks of gannets revealed a progressive increase of the foraging effort, with longer trips in

distance and time during the course of each breeding season (Fig. 5). This suggests that at a local scale, intra-specific competition was still present. By slowly depleting food resources in foraging areas closest to the colony, breeding gannets had to progressively go further and spend more time searching for food (Weber et al., 2021), but not far or long enough to alter their reproductive success.

Overall, our study demonstrates that one single disastrous disease outbreak triggering high mortality rates may not immediately put large populations of long-lived species at risk of extinction. On the contrary, release in density-dependant mechanisms such as intra-specific competition may decrease the effort needed to access natural food resources, which could improve the prospects of the surviving individuals and ultimately help populations recover more quickly (Genton et al., 2012; Hale and Briskie, 2009; Langwig et al., 2012; Ponchon et al., 2024). Such recoveries sometimes even overshoot pre-infection population sizes (Dietz et al., 2024; Höner et al., 2012). This resilience potential may be enhanced when populations hold large numbers of immatures or non-breeders that can rapidly take over vacant breeding sites and breed successfully (Cubaynes et al., 2011; Sceviour et al., 2024; Votier et al., 2008) or when immigrants recruit from surrounding populations (Dietz et al., 2024). However, in seabirds, high mortalities already induced by competition with fisheries (Grémillet et al., 2018), fishery bycatches (Ramírez et al., 2024) or climate change (Jeglinski et al., 2024b), may differentially alter population natural recovery to disease outbreaks and jeopardize their long-term resilience. Furthermore, with the increase of emerging diseases, epidemics can become more recurrent, repeatedly affecting populations and severely limiting their ability to recover. On the longer-term, depleted populations may reach critical thresholds where the number of breeding individuals or chick productivity may not be sufficient enough to maintain a positive demographic growth rate, slowly leading to their extinction (Jeglinski et al., 2023; Jenouvrier et al., 2009). This will notably be the case for some gannet populations of the North East-Atlantic including Rouzic, which are already predicted to face challenging demographic dynamics in the near-future due to

climate change (Jeglinski et al., 2024b).

Monitoring the dynamics and impacts of infectious diseases in wildlife populations is challenging, as their emergence is unpredictable and causes issues regarding the access and manipulation of sick animals. Obtaining epidemiological data either directly through individual sampling and indirectly, through the tracking of individuals, appears to be crucial to investigate how individuals respond behaviourally to disease outbreaks in the short and long-term and how this affects population dynamics (Gamble, 2023; Talmon et al., 2025). This will be particularly essential in the context of the current HPAIV panzootic affecting diverse communities of wild birds and mammals over large geographic areas (Banyard et al., 2024; Peacock et al., 2025).

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CRediT authorship contribution statement

Aurore Ponchon: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pascal Provost:** Writing – review & editing, Data curation. **Alice Bernard:** Writing – review & editing, Formal analysis, Data curation. **Thierry Boulonier:** Writing – review & editing, Funding acquisition, Conceptualization. **Mathilde Lejeune:** Writing – review & editing, Data curation. **Amélie Lescroël:** Writing – review & editing, Data curation. **Jérémy Tornos:** Writing – review & editing, Data curation, Conceptualization. **David Grémillet:** Writing – review & editing, Validation, Project administration, Investigation, Funding acquisition, Conceptualization.

Author contribution

AP, JT, TB and DG designed the study. JT, AB, AL, ML, AP and PP carried out fieldwork. AP processed tracking data with the help of AB. PP provided long-term data of the colony of Rouzic. AP conducted spatial and statistical analyses. AP led the writing of the manuscript. All authors contributed critically to the drafts of the manuscript and gave final approval for publication.

Declaration of competing interest

All authors have nothing to declare.

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Data availability

Tracking data from 2022 and 2023 are available on the public repository Movebank (*Morus bassanus* - Northern gannet - Rouzic France - ID_PROG 536). Previous tracking data (2005 to 2019) are partly available in the Seabird Tracking Database (ID datasets 1793, 734, 1794, 1795, 1796) and are all compiled in the Zenodo archive <https://doi.org/10.5281/zenodo.15212532>. R codes to run the spatial and statistical analyses are freely available on GitHub: <https://github.com/auponchon/NorthernGannets2023>.

[com/auponchon/NorthernGannets2023](https://github.com/auponchon/NorthernGannets2023).

References

- Alexander, D., Brown, I., 2009. History of highly pathogenic avian influenza. *Rev. Sci. Tech.* 28, 19–38. <https://doi.org/10.20506/rst.28.1.1856>.
- Andersson, M., 1994. *Sexual selection*. Princeton University Press, Princeton, NJ.
- Ashmole, N.P., 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b, 458–473. <https://doi.org/10.1111/j.1474-919X.1963.tb06766.x>.
- Banyard, A.C., Bennison, A., Byrne, A.M.P., Reid, S.M., Lynton-Jenkins, J.G., Mollett, B., De Silva, D., Peers-Dent, J., Finlayson, K., Hall, R., Blockley, F., Blyth, M., Falchieri, M., Fowler, Z., Fitzcharles, E.M., Brown, I.H., James, J., 2024. Detection and spread of high pathogenicity avian influenza virus H5N1 in the Antarctic Region. *Nat. Commun.* 15, 7433. <https://doi.org/10.1038/s41467-024-51490-8>.
- Benhamou, S., 2011. Dynamic Approach to Space and Habitat Use Based on Biased Random Bridges. *PLoS One* 6, e14592. <https://doi.org/10.1371/journal.pone.0014592>.
- Bennison, A., Giménez, J., Quinn, J.L., Green, J.A., Jessopp, M., 2022. A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *R. Soc. Open Sci.* 9, 210520. <https://doi.org/10.1098/rsos.210520>.
- Binning, S.A., Shaw, A.K., Roche, D.G., 2017. Parasites and Host Performance: Incorporating Infection into Our Understanding of Animal Movement. *Integr. Comp. Biol.* 57, 267–280. <https://doi.org/10.1093/icb/ixc024>.
- Careen, N.G., Collins, S.M., D'entremont, K.J.N., Wight, J., Rahman, I., Hargan, K.E., Lang, A.S., Montevicchi, W.A., 2024. Highly pathogenic avian influenza resulted in unprecedented reproductive failure and movement behaviour by Northern Gannets. *Mar. Ornithol.* 52, 121–128.
- Clark, B.L., Cox, S.C., Atkins, K.M., Bearhop, S., Bicknell, A.W.J., Bodey, T.W., Cleasby, I.R., Grecian, W.J., Hamer, K.C., Loveday, B.R., Miller, P.I., Morgan, G., Morgan, L., Newton, J., Patrick, S.C., Scales, K.L., Sherley, R.B., Vigfusdóttir, F., Wakefield, E.D., Votier, S.C., 2021. Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. *Mar. Ecol. Prog. Ser.* 661, 1–16.
- Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier, S.C., Bearhop, S., Hamer, K.C., 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar. Ecol. Prog. Ser.* 518, 1–12. <https://doi.org/10.3354/meps11112>.
- Corbett, E.C., Brumfield, R.T., Faircloth, B.C., 2024. The mechanistic, genetic and evolutionary causes of bird eye colour variation. *Ibis* 166, 560–589. <https://doi.org/10.1111/ibi.13276>.
- Crespin, L., Harris, M.P., Lebreton, J.-D., Frederiksen, M., Wanless, S., 2006. Recruitment to a seabird population depends on environmental factors and on population size. *J. Anim. Ecol.* 75, 228–238. <https://doi.org/10.1111/j.1365-2656.2006.01035.x>.
- Cubaynes, S., Doherty, P.F., Schreiber, E.A., Gimenez, O., 2011. To breed or not to breed: a seabird's response to extreme climatic events. *Biol. Lett.* 7, 303–306. <https://doi.org/10.1098/rsbl.2010.0778>.
- Davidson, G.L., Thornton, A., Clayton, N.S., 2017. Evolution of iris colour in relation to cavity nesting and parental care in passerine birds. *Biol. Lett.* 13, 20160783. <https://doi.org/10.1098/rsbl.2016.0783>.
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: A global assessment. *Biol. Conserv.* 237, 525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>.
- Dietz, J.M., Mickelberg, J., Traylor-Holzer, K., Martins, A.F., Souza, M.N., Hankerson, S. J., 2024. Golden lion tamarin metapopulation dynamics five years after heavy losses to yellow fever. *Am. J. Primatol.* 86, e23635. <https://doi.org/10.1002/ajp.23635>.
- Dougherty, E.R., Seidel, D.P., Carlson, C.J., Spiegel, O., Getz, W.M., 2018. Going through the motions: incorporating movement analyses into disease research. *Ecol. Lett.* 21, 588–604. <https://doi.org/10.1111/ele.12917>.
- Duriez, O., Sassi, Y., Le Gall-Ladevèze, C., Giraud, L., Straughan, R., Dauverné, L., Terras, A., Boulonier, T., Choquet, R., Van De Wiele, A., Hirschinger, J., Guérin, J.-L., Le Loc'h, G., 2023. Highly pathogenic avian influenza affects vultures' movements and breeding output. *Curr. Biol.* 33, 3766–3774.e3. <https://doi.org/10.1016/j.cub.2023.07.061>.
- Falchieri, M., Reid, S.M., Ross, C.S., James, J., Byrne, A.M.P., Zamfir, M., Brown, I.H., Banyard, A.C., Tyler, G., Philip, E., Miles, W., 2022. Shift in HPAI infection dynamics causes significant losses in seabird populations across Great Britain. *Vet. Rec.* 191, 294–296. <https://doi.org/10.1002/vetr.2311>.
- Fieberg, J.R., Kochanny, C.O., 2005. Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildl. Manag.* 69, 1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTOI\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTOI]2.0.CO;2).
- Gamble, A., 2023. Disease ecology: When a GPS logger tells you more than a blood sample. *Curr. Biol.* 33, R907–R909. <https://doi.org/10.1016/j.cub.2023.08.018>.
- Genton, C., Cristescu, R., Gatti, S., Levréro, F., Bigot, E., Caillaud, D., Pierre, J.-S., Ménard, N., 2012. Recovery Potential of a Western Lowland Gorilla Population following a Major Ebola Outbreak: Results from a Ten Year Study. *PLoS One* 7, e37106. <https://doi.org/10.1371/journal.pone.0037106>.
- Genton, C., Pierre, A., Cristescu, R., Lévréro, F., Gatti, S., Pierre, J.-S., Ménard, N., Le Gouar, P., 2015. How Ebola impacts social dynamics in gorillas: a multistate modelling approach. *J. Anim. Ecol.* 84, 166–176. <https://doi.org/10.1111/1365-2656.12268>.
- Grémillet, D., Ponchon, A., Paleczny, M., Palomares, M.-L.D., Karpouzi, V., Pauly, D., 2018. Persisting worldwide seabird-fishery competition despite seabird community decline. *Curr. Biol.* 28, 4009–4013. <https://doi.org/10.1016/j.cub.2018.10.051>.

- Grémillet, D., Ponchon, A., Provost, P., Gamble, A., Abed-Zahar, M., Bernard, A., Courbin, N., Delavaud, G., Deniau, A., Fort, J., Hamer, K.C., Jeavons, R., Lane, J.V., Langley, L., Matthiopoulos, J., Poupart, T., Prudor, A., Stephens, N., Trevail, A., Wanless, S., Votier, S.C., Jeglinski, J.W.E., 2023. Strong breeding colony fidelity in northern gannets following high pathogenicity avian influenza virus (HPAIV) outbreak. *Biol. Conserv.* 286, 110269. <https://doi.org/10.1016/j.biocon.2023.110269>.
- Hale, K.A., Briskie, J.V., 2009. Rapid recovery of an island population of the threatened South Island Saddleback *Philesturnus c. carunculatus* after a pathogen outbreak. *Bird Conservation International* 19, 239–253. <https://doi.org/10.1017/S0959270909008193>.
- Hartig, F., 2021. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models (R package).
- Herrera, J., Nunn, C.L., 2019. Behavioural ecology and infectious disease: implications for conservation of biodiversity. *Philos. Trans. R. Soc. B* 374, 20180054. <https://doi.org/10.1098/rstb.2018.0054>.
- Höner, O.P., Wachter, B., Goller, K.V., Hofer, H., Runyoro, V., Thierer, D., Fyumagwa, R. D., Müller, T., East, M.L., 2012. The impact of a pathogenic bacterium on a social carnivore population. *J. Anim. Ecol.* 81, 36–46. <https://doi.org/10.1111/j.1365-2656.2011.01873.x>.
- Jeglinski, J.W.E., Lane, J.V., Votier, S.C., Furness, R.W., Hamer, K.C., McCafferty, D.J., Nager, R.G., Shedd, M., Wanless, S., Matthiopoulos, J., 2024a. HPAIV outbreak triggers short-term colony connectivity in a seabird metapopulation. *Sci. Rep.* 14, 3126. <https://doi.org/10.1038/s41598-024-53550-x>.
- Jeglinski, J.W.E., Niven, H.I., Wanless, S., Barrett, R.T., Harris, M.P., Dierschke, J., Matthiopoulos, J., 2024b. Past and future effects of climate on the metapopulation dynamics of a Northeast Atlantic seabird across two centuries. *Ecol. Lett.* 27, e14479. <https://doi.org/10.1111/ele.14479>.
- Jeglinski, J.W.E., Wanless, S., Murray, S., Barrett, R.T., Gardarsson, A., Harris, M.P., Dierschke, J., Strøm, H., Lorentsen, S.-H., Matthiopoulos, J., 2023. Metapopulation regulation acts at multiple spatial scales: Insights from a century of seabird colony census data. *Ecol. Monogr.* 93, e1569. <https://doi.org/10.1002/ecm.1569>.
- Jenouvrier, S., Barbraud, C., Weimerskirch, H., Caswell, H., 2009. Limitation of population recovery: a stochastic approach to the case of the emperor penguin. *Oikos* 118, 1292–1298. <https://doi.org/10.1111/j.1600-0706.2009.17498.x>.
- Katzenberger, J., Gottschalk, E., Balkenhol, N., Waltert, M., 2021. Density-dependent age of first reproduction as a key factor for population dynamics: stable breeding populations mask strong floater declines in a long-lived raptor. *Anim. Conserv.* 24, 862–875. <https://doi.org/10.1111/acv.12687>.
- Kranstauber, B., Smolla, M., Scharf, A.K., 2023. move: Visualizing and Analyzing Animal Track Data.
- Lane, J.V., Jeglinski, J.W.E., Avery-Gomm, S., Ballstaedt, E., Banyard, A.C., Barychka, T., Brown, I.H., Brugger, B., Burt, T.V., Careen, N., Castenschiöld, J.H.F., Christensen-Dalsgaard, S., Clifford, S., Collins, S.M., Cunningham, E., Danielsen, J., Daunt, F., D'entremont, K.J.N., Doiron, P., Duffy, S., English, M.D., Falchieri, M., Giacinti, J., Gjerset, B., Granstad, S., Grémillet, D., Guillemette, M., Hallgrímsson, G.T., Hamer, K.C., Hammer, S., Harrison, K., Hart, J.D., Hatsell, C., Humpidge, R., James, J., Jenkinson, A., Jessopp, M., Jones, M.E.B., Lair, S., Lewis, T., Malinowska, A.A., McCluskie, A., McPhail, G., Moe, B., Montevicchi, W.A., Morgan, G., Nichol, C., Nisbet, C., Olsen, B., Provencher, J., Provost, P., Purdie, A., Rail, J.-F., Robertson, G., Seyer, Y., Shedd, M., Soos, C., Stephens, N., Strøm, H., Svansson, V., Tierney, T.D., Tyler, G., Wade, T., Wanless, S., Ward, C.R.E., Wilhelm, S.I., Wischniewski, S., Wright, L.J., Zonfrillo, B., Matthiopoulos, J., Votier, S.C., 2024. High pathogenicity avian influenza (H5N1) in Northern Gannets (*Morus bassanus*): Global spread, clinical signs and demographic consequences. *Ibis* 166, 633–650. <https://doi.org/10.1111/ibi.13275>.
- Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H., Marm Kilpatrick, A., 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecol. Lett.* 15, 1050–1057. <https://doi.org/10.1111/j.1461-0248.2012.01829.x>.
- Le Bot, T., Lescroët, A., Fort, J., Péron, C., Gimenez, O., Provost, P., Grémillet, D., 2019. Fishery discards do not compensate natural prey shortage in Northern gannets from the English Channel. *Biol. Conserv.* 236, 375–384. <https://doi.org/10.1016/j.biocon.2019.05.040>.
- Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., 2002. Sex-Specific Foraging Behaviour in a Monomorphic Seabird. *Proc. Biol. Sci.* 269, 1687–1693.
- Patterson, A., Gilchrist, H.G., Benjaminsen, S., Bolton, M., Bonnet-Lebrun, A.S., Davoren, G.K., Descamps, S., Erikstad, K.E., Frederiksen, M., Gaston, A.J., Gulka, J., Hentati-Sundberg, J., Huffeldt, N.P., Johansen, K.L., Labansen, A.L., Linnebjerg, J.F., Love, O.P., Mallory, M.L., Merkel, F.R., Montevicchi, W.A., Mosbech, A., Olsson, O., Owen, E., Ratcliffe, N., Regular, P.M., Reiertsen, T.K., Røpelt-Coudert, Y., Strøm, H., Thórarinnsson, T.L., Elliott, K.H., 2022. Foraging range scales with colony size in high-latitude seabirds. *Curr. Biol.* 32, 3800–3807.e3. <https://doi.org/10.1016/j.cub.2022.06.084>.
- Peacock, T.P., Moncla, L., Dudas, G., VanInsberghe, D., Sukhova, K., Lloyd-Smith, J.O., Worobey, M., Lowen, A.C., Nelson, M.I., 2025. The global H5N1 influenza panzootic in mammals. *Nature* 637, 304–313. <https://doi.org/10.1038/s41586-024-08054-z>.
- Phillips, R.A., Fort, J., Dias, M.P., 2023. Chapter 2 - Conservation status and overview of threats to seabirds. In: Young, L., VanderWerf, E. (Eds.), *Conservation of Marine Birds*. Academic Press, pp. 33–56. <https://doi.org/10.1016/B978-0-323-88539-3.00015-7>.
- Pinheiro, J., Bates, D.M., 2023. nlme: Linear and Nonlinear Mixed Effects Models. R Core Team (2023).
- Ponchon, A., Choquet, R., Martins, A.F., Ruiz-Miranda, C.R., Albert, C.H., Romano, V., 2024. Yellow fever outbreak temporarily changes dispersal patterns in an endangered primate. <https://www.preprints.org/manuscript/202403.0832/v3>.
- R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Ramírez, I., Mitchell, D., Vulcano, A., Rouxel, Y., Marchowski, D., Almeida, A., Arcos, J. M., Cortes, V., Lange, G., Morkūnas, J., Oliveira, N., Paiva, V.H., 2024. Seabird bycatch in European waters. *Anim. Conserv.* 27, 737–752. <https://doi.org/10.1111/acv.12948>.
- Sceviour, M.P., Ward, C.R.E., Wilhelm, S.I., 2024. Immature Northern gannets (*Morus bassanus*) increase colony attendance following highly pathogenic avian influenza. *Ibis*. <https://doi.org/10.1111/ibi.13390> n/a.
- Smith, K.F., Acevedo-Whitehouse, K., Pedersen, A.B., 2009. The role of infectious diseases in biological conservation. *Anim. Conserv.* 12, 1–12. <https://doi.org/10.1111/j.1469-1795.2008.00228.x>.
- Smith, K.F., Sax, D.F., Lafferty, K.D., 2006. Evidence for the Role of Infectious Disease in Species Extinction and Endangerment. *Conserv. Biol.* 20, 1349–1357. <https://doi.org/10.1111/j.1523-1739.2006.00524.x>.
- Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E., Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J., Votier, S.C., 2012. Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. *Mar. Ecol. Prog. Ser.* 457, 151–162.
- Talmon, I., Pekarsky, S., Bartan, Y., Thie, N., Getz, W.M., Kamath, P.L., Bowie, R.C.K., Nathan, R., 2025. Using wild-animal tracking for detecting and managing disease outbreaks. *Trends Ecol. Evol.* 40, 760–771. <https://doi.org/10.1016/j.tree.2025.05.004>.
- Tellier, R., 2006. Review of aerosol transmission of Influenza A Virus. *Emerg. Infect. Dis.* 12, 1657–1662.
- Thomas, F., Renaud, F., De Meëus, T., Cézilly, F., 1995. Parasites, Age and the Hamilton-Zuk Hypothesis: Inferential Fallacy? *Oikos* 74, 305–309. <https://doi.org/10.2307/3545660>.
- van Gils, J.A., Munster, V.J., Radersma, R., Liefhebber, D., Fouchier, R.A.M., Klaassen, M., 2007. Hampered Foraging and Migratory Performance in Swans Infected with Low-Pathogenic Avian Influenza A Virus. *PLoS One* 2, e184. <https://doi.org/10.1371/journal.pone.0000184>.
- Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H., Hatchwell, B.J., 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *J. Anim. Ecol.* 77, 974–983. <https://doi.org/10.1111/j.1365-2656.2008.01421.x>.
- Wakefield, E.D., Cleasby, I.R., Bearhop, S., Bodey, T.W., Davies, R.D., Miller, P.I., Newton, J., Votier, S.C., Hamer, K.C., 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology* 96, 3058–3074. <https://doi.org/10.1890/14-1300.1>.
- Weber, S.B., Richardson, A.J., Brown, J., Bolton, M., Clark, B.L., Godley, B.J., Leat, E., Oppel, S., Shearer, L., Soetaert, K.E.R., Weber, N., Broderick, A.C., 2021. Direct evidence of a prey depletion “halo” surrounding a pelagic predator colony. *Proc. Natl. Acad. Sci.* 118, e2101325118. <https://doi.org/10.1073/pnas.2101325118>.
- Wille, M., Barr, I.G., 2022. Resurgence of avian influenza virus. *Science* 376, 459–460. <https://doi.org/10.1126/science.abo1232>.