

HPAIV outbreak triggers long-distance movements in breeding Northern gannets – implications for disease spread

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Abstract

Animal movement is a fundamental driver of disease spread. We show that an outbreak of high pathogenicity avian influenza (HPAI) is coincident with unprecedented behavioural changes in GPS tracked Northern gannets. Previously characterised by strong fidelity to their nest sites and foraging areas (2015 – 2019; n = 120), breeding gannets tracked before, during and after the 2022 outbreak showed half of ten birds stopped transmitting and most likely died, while the survivors instigated unusual long-distance movements. Two adults visited one - three other gannetries – the first such incidence of prospecting in this age class. Our findings suggest the HPAIV outbreak triggered changes in space use patterns of possibly infected individuals that amplified the epidemiological connectivity among colonies and may generate super-spreader events that accelerate disease transmission across the metapopulation. Such self-propagating transmission from and towards high density animal aggregations may explain the rapid pan-European spread of HPAIV in the gannet.

Running title: HPAIV outbreak modifies gannet space use patterns

HPAIV outbreak triggers long-distance movements in breeding Northern gannets – implications for disease spread

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Author statement: JJ and RN conceived the original study for which the data was collected, in discussion with DMC and SW; JJ, JL, RWF, MS and SV collected the GPS tracking data in 2022 and JL and KM supplied GPS tracking data from previous years; JJ and JM interpreted the data in the context of the HPAIV outbreak and designed the analysis, JJ analysed the data; JJ wrote the manuscript with support from JL, SV and JM, all co-authors contributed critically to the final version.

Keywords: avian influenza, bio-logging, conservation, disease ecology, information centre, metapopulation, *Morus bassanus*, pathogen spread, seabird, super-spreading events

Data accessibility statement: Upon publication and with an embargo period of one year, the data that support the findings of this study are openly available in the Movebank repository at www.movebank.org, reference number 2658220054 and 2658117564 and, upon request, from the Seabird Tracking database.

Code to access the data used in the analysis, to run the analyses and to generate the figures in this manuscript is supplied in the GitHub repository https://github.com/JanaJeglinskiR/gannet_movements_HPAIV

and will be made publicly available with a doi on Zenodo upon publication.

Abstract

Animal movement is a fundamental driver of disease spread. We show that an outbreak of high pathogenicity avian influenza (HPAI) is coincident with unprecedented behavioural changes in GPS tracked Northern gannets. Previously characterised by strong fidelity to their nest sites and foraging areas (2015 – 2019; n = 120), breeding gannets tracked before, during and after the 2022 outbreak showed half of ten birds stopped transmitting and most likely died, while the survivors instigated unusual long-distance movements. Two adults visited one - three other gannetries – the first such incidence of prospecting in this age class. Our findings suggest the HPAIV outbreak triggered changes in space use patterns of possibly infected individuals that amplified the epidemiological connectivity among colonies and may generate super-spreader events that accelerate disease transmission across the metapopulation. Such self-propagating transmission from and towards high density animal aggregations may explain the rapid pan-European spread of HPAIV in the gannet.

Introduction

Animal movement is a fundamental driver of disease spread in domestic and wild species . Individuals regularly move across the landscape for multiple purposes including foraging, dispersal and migration. During migration, animals perform regular long-distance movements across large spatial scales, congregate in high densities at stopover sites and thus may carry diseases to geographically distant locations and habitats . For example, migrating wild ducks, geese and swans appear to have introduced High Pathogenicity Avian influenza (HPAI H5Nx) from Asia to Europe, Russia, Africa and North America over the last two decades . Dispersing or prospecting movements of animals occur over smaller spatial scales, connect different subpopulations and can facilitate disease spread between them . Further, foraging movements have the potential to influence disease ecology and transmission via inter-population overlap, but are poorly studied in this context. The latter appears particularly pertinent for central-place foraging animals such as pinnipeds, bats and seabirds where animals breed in segregated high-density colonies but forage widely with the potential to transmit diseases. In seabirds, some species forage in areas that overlap between neighbouring colonies whereas others have colony-specific non-overlapping foraging ranges . These differences are likely to influence disease transmission risk among colonies. Furthermore, many animal species display age- and stage-specific movement patterns that influence their propensity for disease transmission. For example, prospecting is a behaviour that entails visits by individuals to breeding areas where they do not currently breed but might settle in the future . In seabirds, the behaviour is characteristic for immatures, failed breeders or nonbreeders

whereas breeders are typically faithful to their breeding, foraging and wintering sites within and between years .

Disease may also trigger changes in movement behaviour that influence onward transmission. Studies on experimentally immune-challenged or infected animals have shown that sick animals may become more lethargic (Adelman et al 2010), reduce the complexity of their movements and foraging behaviour and move slower and for shorter distance . Such reduced movement can lower social network connectivity and disease containment . Conversely, there is also evidence for a lack of lethargy in sick birds despite elevated immune responses to a pathogen. Of course, under the extreme scenario of a highly lethal disease outbreak, many animals simply die in mass mortality events . However, beyond the direct physiological effects of disease on the affected animal, outbreaks also alter and disturb the environment that surviving animals inhabit. For example, breeding sites may be littered with sick, dying and dead animals, these deaths may lead to changes in the density and distribution of breeding sites or territories and facilitate access by predators through thinning of previously dense breeding aggregations. All these cues are very likely perceivable to surviving animals and thus may impact their behaviour. Disturbances can drastically alter the behaviour and movement of healthy individuals , as evidenced by global patterns across species of modifications to movement and space use or shifting activity patterns towards nocturnality due to human disturbances . Movement responses can be as deleterious as evasion movements of cetaceans disturbed by naval sonar exercises that lead to mass stranding events or so evidently different from normal behaviour that changes in movement behaviour have been proposed as early warning signals to the presence of poachers . Changes to animal movement patterns as response to disturbances can also have pronounced consequences for the transmission of diseases. For example, logging of forest increased the use of agricultural/farmland in long-tailed macaques, *Macaca fascicularis* , that tested positive for *Plasmodium knowlesi* , thus increasing disease transmission to humans . Culling, as an effort to control disease, instead promoted pathogen spatial spread in vampire bats, *Desmodus rotundus* , and badgers, *Meles meles* , since the disturbance associated with culling increased dispersal . However, questions remain over the possibility for positive feedbacks between infection, mobility and subsequent increased transmissivity. Evidence for the potential of self-propagation of disease through changes in animal movement associated with the disturbance generated by disease outbreaks is rare, probably because monitoring fine-scale animal movement rarely coincides with such unpredictable events.

During spring and summer 2022, an unprecedented HPAIV outbreak dramatically impacted the global metapopulation of Northern gannets *Morus bassanus* (hereafter gannet), with tens of thousands of birds dying in the Northwest and Northeast Atlantic (Lane et al. submitted, . On the 4th June 2022, the first clinical symptoms of HPAIV were observed on the Bass Rock, UK (M. Sheddan, pers. obs.), the world's largest gannet colony with ~ 75,000 breeding pairs . Subsequent tissue analysis from four gannets by the Animal and Plant Health Agency (APHA) confirmed that all birds were positive for clade 3.2.4.4b HPAIV H5N1 (Lane et al., submitted). The disease outbreak rapidly devastated the colony over the course of the following month, reducing the breeding population by 72 %, suppressing adult survival to 0.455 % (compared to 0.94 - 0.95 in previous years; Lane et al . 2020, Wanless et al. 2010), and breeding success to 0.25% compared to 0.72 % in normal years Lane et al. submitted). HPAIV spread rapidly across the entire gannet metapopulation and affected all monitored colonies (40 out of 53) bar one (Lane et al. submitted), but the transmission dynamics and likely vectors of transmission are unknown.

The movement ecology of adult breeding gannets, particularly from Bass Rock, is exceptionally well studied with satellite and GPS tracking from 1998 and many years to the present . Adult gannets are highly site-faithful, returning each year to the same colony and mostly the same nest site . If a breeding attempt fails, birds continue nest site ownership (Lane et al pers. obs.) and maintain a regular routine of commuting between colony and foraging sites at sea . Incubating and chick-rearing birds display highly predictable movements to individual-specific foraging areas . The gannet is one of the species that has been shown to forage in colony-specific, non-overlapping foraging ranges during the breeding season (Wakefield et al 2013). Taken together, these space use characteristics suggest limited potential for contact among breeding colonies, making adult gannets unlikely candidates for disease transmission across the metapopulation.

Here, we investigate the impact of an HPAIV outbreak on the short-term adult gannet movement behaviour before, during and shortly after the epidemic at Bass Rock. By using GPS-GSM devices we show that adult gannets drastically changed their space use patterns concomitant with the outbreak. These movement behaviour modifications increased the potential for inter-colony contact, both at sea and on land, and might have directly contributed to the rapid transmission of HPAIV across the gannet metapopulation, through multiple direct or indirect contact routes.

Materials and methods

GPS tracking – 2022 (HPAIV year)

We captured five breeding pairs of gannets on 29th and 30th April 2022 at Bass Rock, UK (56° 04', 2° 29'), about one month before the HPAIV outbreak at this colony. Territorial pairs were caught before egg-laying (Jeglinski et al, in prep.). We also captured 10 breeding adults with 2 – 8 weeks old chicks between the 11th – 14th August 2022, about 2.5 months after the start of the HPAIV outbreak on the Bass Rock. A detailed analysis of the August dataset is described in Grémillet et al. (in review).

For the captures, we used a 6 m telescopic pole with a hook or noose attached to the end and restrained the birds in a custom-designed 'gannet-jacket' that allows efficient handling and weighing to minimize capture stress for the bird. We weighed birds with a digital scale (Kern, precision 0.1 kg), and took morphometric measurements with a metal ruler (precision 1 cm) and a digital calliper (precision 0.01 mm), respectively. As far as possible, we targeted previously colour-ringed birds with known successful breeding status in previous years, and ringed unmarked birds with a British Trust for Ornithology metal ring and a blue-white high impact acrylic colour ring with a unique alphanumeric combination. Birds were assumed to form a pair because they performed courtship behaviours and attended the same breeding site and all pairs consisted of at least one previously marked individual so that the sex of each bird was known or inferred based on the sex of its partner. We attached nanofix GPS GSM tags (Pathtrack Ltd., Otley, UK, 18g) to the central three tail feather using TESA 4651 tape. Tags were programmed to record the birds' location every 15 minutes and scheduled to send 12-hourly data packages via the mobile phone network to a server, from where we accessed data in near real-time. The tags are solar powered and have a built-in dynamic algorithm that adjusts the GPS fix frequency depending on battery charge.

The total handling time lasted ~ 10 minutes. Once released, most birds returned immediately to their nests. We monitored all birds after capture and on subsequent trips to verify pair continuity and nest status. We confirmed in late May that all pairs tagged in April were incubating an egg. One pair had split up or been erroneously captured as a pair, but both birds were incubating an egg with unmarked partners. Access to the colony following the August captures was restricted due to the HPAIV outbreak, but we resighted one GPS tagged bird captured in August with a chick in late September – the others were not resighted, but chicks might have already fledged at this late stage of the breeding season.

GPS tracking – non HPAIV years

For comparison with the data from the HPAIV year 2022, we used GPS tracking data for incubating or breeding Bass Rock gannets collected during 2015 – 2019 (150 deployments; n = 120 individual birds). Briefly, the capture methodology was very similar to the approach we took in 2022, but instead of GPS-GSM tags, small GPS loggers (igotU-GT600, Mobile Action Technology, Taipei, Taiwan, 33 g) with a fixed sampling interval of 2 minutes were deployed, both before incubation in late April (2017 – 2019) and at chick rearing from mid-July (2015 – 2019). Tags deployed on birds during April were retrieved mainly in June, tags deployed during chick-rearing were retrieved after 7 - 14 days .

Maximum daily distance to capture colony

Prior to any spatial data analyses, we transformed all spatial data into the Lambert Azimuth Equal Area LAEA (EPSG code 3035) projection. We curtailed GPS data to the 30th September 2022 to omit GPS locations associated with the onset of migration.

We calculated the maximum daily distance to the Bass Rock breeding colony as a measure of the extent of the space used by each bird. First, using the function *gridDistance* (R package raster, Hijmans, 2022), we generated a distance raster with a resolution of 1 km that originated at the Bass Rock and that excluded land thus reflecting biologically realistic travel distances. Overlaying the GPS locations on the distance raster, we extracted the distance (measured in km) of each GPS location to the Bass Rock using the function *st_extract* (R package stars, Pebesma, 2022). We calculated the ‘julian day’ of each GPS location using the function *yday* (R package lubridate, Grolemund & Wickham 2011) and used the maximum distance for each day, for each bird in each year as response variable for our model. Prior to the statistical analysis (see below), we filtered the dataset to include only maximum distances > 0 , to omit colony visits.

Colony visits

For each GPS location, we calculated the nearest distance to any known gannet breeding colony using the *st_nn* function (R package ngeo, Dorman, 2022). Since gannets congregate in ‘rafts’ in the vicinity of colonies and the majority of rafting events were concentrated within a 2 km radius around a colony, we defined a ‘colony visit’ as a visit of more than 15 minutes (two subsequent GPS locations for 2022 and seven for previous years when sampling rate was higher) within a 2 km radius of a gannet breeding colony. We retained the identity of any visited colony and calculated the duration of the colony visit as the difference between the earliest timestamp of a GPS location within the 2 km radius and the first timestamp of the subsequent location outside of it.

Statistical analysis

We fitted a mixed-effect generalised additive model using the function *gam* (R package mgcv, to the data to quantify potential non-linear variation in the relationship between ‘maximum daily distance’ (response variable) and Julian day (explanatory variable). We fitted an interaction between smoothed Julian-day and the factor ‘HPAIV status’, classifying all years prior to 2022 as ‘non-HPAIV’ and the year 2022 as “HPAIV”. We accounted for the non-independence of repeated data points from the same bird by fitting a random effect for Bird ID on the intercept.

We used R version 4.2.2 (R Core Team, 2021) for all data processing and analyses.

Results

Fate of breeding gannets tagged during the HPAIV outbreak

GPS transmission for five birds, three males and two females, each from a different pair, ended abruptly, only 3.4 ± 2.9 days after the outbreak started on the 4th of June 2022 (range -1 – 6 days, Figure 1D). Since tail-mounted TESA deployments can last up to five months (J. Jeglinski, unpublished), these short transmission periods suggest that the birds died and that all pairs were broken up by the death of one partner. Indeed, one of these birds (Bird Id 18244) was found long dead in Swedish waters on the 21st July 2022 (Figure 1D). The remaining birds transmitted data for 42 ± 35.8 days following the outbreak (range 18 – 101 days, Figure 1D). Three (18220, 18233, 18247) out of the 10 birds tagged in April prior to incubation were sighted alive during subsequent visit to the colony 58, 111 and 112 days after the start of the outbreak, respectively; all three birds had lost the GPS tag and 18220’s right eye had turned black (Figure 1D).

Variation in maximum movement range in HPAIV and non HPAIV years

Breeding gannets that survived the first few days of the outbreak instigated long-distance movements away from the Bass Rock on the 4th June ($n = 5$ individuals, mean \pm sd, 369 ± 221 km, max 933 km, Figure 1 A, B). These differed from the regular trips during the incubation period before the outbreak, after the peak of the outbreak from August 2022 onwards, and also from the regular trips during incubation and chick rearing in 2015 - 2019 (Figure 1A, B). The interaction between Julian day and the year’s HPAIV status was highly significant (Julian day:HPAIV year, edf = 8.21, $F = 30.41$, $p < 0.01$; Julian day: non-HPAIV year, edf = 4.42, $F = 12.62$, $p < 0.01$), suggesting that the slopes of the non-linear relationship between Julian day and maximum daily distance differed significantly between 2022 and all previous years (Figure 1

E). In 2015-2019, birds travelled further from the colony during incubation than whilst chick-rearing, with maximum distances peaking in late May (before 4th June or Julian day 155) before decreasing and levelling off over time as chick-rearing progressed (Figure 1C). In the HPAIV year, birds continued to increase the maximum distance travelled from the colony through June while the HPAIV outbreak was ongoing on Bass Rock. Their maximum distances from the colony peaked in mid-July and decreased to below incubation-period distances around 2.5 months after the onset of the outbreak, to increase again towards the end of the breeding season (Figure 1E).

Colony visits

During the HPAIV outbreak (i.e. between 4th June and 31st July), two of the surviving GPS-tracked gannets visited other colonies, with one bird (bird ID 18247m female) visiting three colonies (Troup Head, St. Kilda, and Ailsa Craig), and a second (bird ID 18220, female) visiting Heligoland (Figure 1 B, SM1 Figure S1 – S5). A third bird (bird ID 18226, male) flew to the Norwegian coast, moved ~ 50 km inland, visiting several freshwater lakes, then returned to the coast where transmission ceased (Figure 1 B, SM1 Figure S6 - S7). None of the 120 birds tracked between 2015 and 2019 visited a different breeding colony. None of the other GPS tracked gannets has ever been recorded flying inland and frequenting freshwater bodies.

Discussion

We found evidence that surviving adult breeding gannets that had lost their egg/chick and likely also their partner at the start of the HPAIV outbreak on the Bass Rock modified their regular movement and space use patterns by instigating long-distance movements towards geographic locations beyond well-documented previous ranges, including visiting inland freshwater lakes and prospecting several other gannet breeding colonies.

Prospecting provides colonial animals with information on site quality, which can inform recruitment . In seabirds, adults tend to be philopatric following recruitment and prospecting is primarily associated with immatures . However, breeding failure may initiate prospecting in some instances, although evidence points primarily towards Laridae which frequently breed in ephemeral habitats (e.g. coastal shingle) and thus tend to have lower philopatry than other seabird taxa . In contrast, gannet colonies are more stable over time, some having existed for hundreds of years . Indeed, based on data from the many hundreds of breeding gannets tracked from 16 colonies over more than two decades, we are unaware of any similar prospecting or wide-ranging movements by adults (e.g., Hamer, 2000, 20001, 2007, 2009, Lane 2020, Garthe 2007, Waggitt 2014, Votier 2017, Warwick Evans 2015, Clark 2019, Pettex 2012, Gremillet 2006, Wakefield 2013, Peschko 2021). Previous tracking of failed breeders revealed they are less constrained than breeders but did not show the long-distance and inter-colony movements described here (Votier et al 2017). Moreover, Cape gannets, *Morus capensis* maintain nest sites and foraging ranges under extreme food stress and mass breeding failure . Gannets acquire their breeding sites over a period of years, which often involves vigorous fighting and near-continuous displaying and it is possible that the high investment involved in this prolonged process may generally not be traded off against rushed site abandonment. It appears that the outbreak of a highly lethal disease, and the resulting severe and obvious decay in the quality of the breeding habitat around them, may be a sufficiently drastic disturbances to their environment that has the potential to decrease the site faithfulness of gannets.

The HPAIV outbreak triggered long-distance movements of gannets into geographic areas that breeding gannets did not frequent before or after the outbreak or in any of the five other years we had tracking data for the study colony. ‘Fleeing’ is one of several behaviours that animals may show in response to a disturbance . However, direct responses to the disturbance caused by disease outbreaks are poorly understood since this requires serendipitous animal observations or tracking concurrent with severe disease outbreaks. One rare example is a record of long-distance movements of a white-tailed deer, *Odocoileus virginianus* , away from a chronic wasting disease outbreak which may serve as rapid long-distance dispersal mechanism of the disease . Similarly, unusual long-distance migratory movements of harp seals *Phoca gronelandica* may have brought morbillivirus into the European harbour seal *Phoca vitulina* population, and long-distance movements of

asymptomatic grey seals, *Halichoerus gryphus* , may have spread the virus across large geographic scales, resulting in two severe phocine distemper outbreaks with thousands of dead seals in the last three decades . At the height of the HPAIV outbreak, disorientated sick gannets that later died have been observed at highly unusual inland locations, for example on a farm in Dorset (N. Baker, in litt.) and it is possible that the gannet movements towards inland Norway illustrate such a case.

Long-distance movements are only relevant for disease transmission dynamics if the moving animal is infectious at the time of movement. We do not have these data for our GPS-tracked gannets since they were captured well before the disease outbreak. However, the GPS-tracked animals nested in an area where we recorded severe mortality of adult breeders (Lane et al. submitted), where gannets, incapacitated by clinical HPAIV symptoms such as uncontrollable body jerks and spasms, tumbled through the breeding birds and were attacked by breeders leading to direct physical contact (Clifford. S, pers. obs.). It is highly likely that the GPS tracked birds were exposed to the virus, also evidenced by the immediate cessation of data transmission and likely death of half of our study birds. The duration of viral shedding for HPAIV for seabirds is unknown, but data from six experimentally infected wild duck species suggests that live virus can be shed from 1-2 days after inoculation, for periods between 5 and 14 days . Surviving gannets in our study travelled rapidly over the course of a few days to novel locations during the HPAIV outbreak, thus may well have been infectious over that period.

The unusual long-distance movements described above involved gannets spending time in other gannet colonies and in foraging ranges of gannets from other colonies as well as visiting inland lakes, which may have brought a sick gannet into contact with waterfowl that gannets would normally never have encountered. Given our small sample size, the number of birds that performed these movements is astonishingly high. If the individual-level responses we describe here scale up to the colony level, the outbreak of HPAIV may self-propagate transmission through the gannet metapopulation, and potentially beyond, by altering gannet movement that enhance the connectivity between different gannet colonies and different habitat types with different susceptible animal communities. Long-distance movements in diverse directions across the metapopulation have the potential to lead to superspreading events . In disease ecology, super spreaders are individuals that are responsible for disproportionately large numbers of secondary cases , for example through increased contact rates. Super spreaders have the potential to profoundly alter disease dynamics because they play a pivotal role in the shaping the speed, distance and magnitude of epidemics . In the specific case of the HPAIV epidemic in gannets, such super-spreading, even by a small number of individuals, might explain the rapid spread through the gannet colony networks in the West and East Atlantic (Lane et al., submitted).

Our data suggest that the potential for super spreading in gannets coincides with high virus circulation in colonies immediately following the outbreak, but that such unusual movements appear to be short-term responses rather than longer-term behavioural modifications (Figure 1 B, C, E). Indeed, breeding gannets with chicks tracked several months after the onset of HPAIV outbreaks in three gannet colonies did not show any of the unusual space use patterns we found (Grémillet et al. in review). It gives hope that the few breeding pairs with chicks that survived appeared to maintain their established routines, but it remains to be seen if a previous HPAIV infection may have other sub-lethal effects on behaviour and physiology of surviving gannets in coming years.

Conclusions

In 2022, HPAIV emerged, unexpectedly, which poses a severe threat to the global gannet metapopulation and many other seabird species . Modelling of avian cholera, a similarly threatening disease in common eiders *Somateria mollissima* , has shown that, at one colony, 30% mortality and more than four outbreaks per decade will lead to extinction in 20 years . Gannet mortality in 2022 at Bass Rock was $> 50\%$ (Lane et al. submitted) - if such mortality events reoccur, the future for gannets looks bleak . Here we show that adult gannets exhibit unusual movement behaviour during the HPAIV outbreak and have the potential to act as super spreaders. Ignoring fine-scale animal movements during disease outbreaks can mis-characterize transmission risk and epidemiological dynamics . To better understand HPAIV transmission dynamics, within and

between species, therefore requires collecting fine-scale movement data from populations at risk across large spatial scales, in combination with epidemiological sampling, demographic monitoring and epidemiological modelling.

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Permits

The fieldwork was performed in partnership with the Scottish Seabird Centre with permission of the landowner of the Bass Rock, Sir Hew Dalrymple, and under a special methods endorsement and ringing permit of the British Trust for Ornithology BTO to Jana Jeglinski. Colour ringing was performed under a permit to Jude Lane from the BTO. We conducted our fieldwork under an exemption to the general ringing ban in seabird colonies granted by NatureScot which permitted us to capture and tag gannets during the HPAIV outbreak. All fieldwork was performed with the required risk assessments and ethical approval in place.

Competing Interests

The authors declare no conflict of interest.

References

Figure headers

Figure 1 A) Movements of breeding adult gannets before the outbreak of HPAIV on the Bass Rock on the 4th of June, B) during the outbreak up until 31st July and C) after the outbreak. Gannets GPS-tracked from April 2022 onwards are individually coloured (see legend), positions for gannets tagged in 2015 – 2019 and from August 2022 in grey. Colony locations are indicated as open black diamonds, colonies visited by GPS tracked birds are shown as orange diamonds D) Maximum daily distances from the Bass Rock colony for gannet pairs tracked during the HPAI outbreak, individual colours correspond with movement data in A, B and C. The vertical black line indicates the start of the HPAIV outbreak on the Bass Rock. E) The relationship between maximum daily distance and Julian day for all other years (left) and the HPAI year (right, gam prediction and confidence interval and raw data)

