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The Role of Climate Conditions on Arctic Tern Population Dynamics

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The Role of Climate Conditions on Arctic Tern Population Dynamics

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Abstract

Arctic terns have been identified as a species that could be particularly vulnerable to the effects of climate change, due to their dependance on global wind systems and multiple areas of marine productivity to support all stages of their life cycle. Despite having knowledge of key feeding areas and conditions that can affect arctic tern foraging, the anticipated effects of climate change on global populations are still uncertain due to variation in pressures faced by different tern colonies, but also the potential ability of this species to adapt through flying long distances and covering large ranges. This study investigated the potential links between climate conditions during the breeding and non-breeding seasons and their effects on demographics of arctic terns on The Skerries, Anglesey, the UK's largest arctic tern colony. Results from a short-term provisioning study and analysis of long-term data on adult survival and productivity were used to assess vulnerabilities of this species to climate variation at different stages of their annual life cycle. Wave height was found to limit chick provisioning during the breeding season when it exceeded an optimal range, which in the future could contribute to reduced productivity in years where colonies experience prolonged episodes or frequent days of high waves during the peak chick rearing period. No patterns were observed with adult survival and climate indices across all periods which could suggest tern survival is not currently affected by annual variation in climate conditions, although some limitations with the ringing data were identified during analysis which could be improved upon in future tag deployments and through a longer dataset. Also, a non-significant but distinct non-linear relationship was identified between NAO in the months immediately prior to the breeding season and subsequent chick productivity that year, suggesting pre-breeding climate conditions could be an important factor in determining colony breeding success and warrants further targeted study. This study highlights the complexities of interactions between animals and environmental conditions in highly migratory species, but that collection and analysis of long-term datasets can offer insights into the main processes driving population-level processes.

Keywords: Arctic tern, foraging, productivity, provisioning, adult survival, breeding condition, migration, weather, climate change.

Declaration

I hereby declare that this thesis is the result of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. I confirm that I am submitting this work with the agreement of my supervisor.

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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Contents

1 Introduction

Long-term increases in average global temperatures, rainfall and winds over the past century, which depict the main observations of climate change (Nicholls et al., 1996), have occurred rapidly beyond natural occurrence and have largely been attributed to the increase in human activities which emit greenhouse gases (EC, 2023). Most regions are experiencing changes to climate at varying degrees, with areas close to the equator and poles currently experiencing the highest levels of change (Harvey et al, 2013). Consequences for wildlife communities in these regions are already being observed through mass mortalities and reproductive failures following extreme weather events (Moreno and Møller 2011), and reactive mitigation strategies are being sought, with policy and legislation at the forefront. To evaluate the ability of policy to provide appropriate mitigation for wildlife communities in climate sensitive ecosystems, it is first important to identify impacts of climate change on species populations, where understanding responses to environmental variation is key (Weiskopf, 2020).

Physical processes within the earth's atmosphere and oceans have a key role in determining weather and climate through ocean mixing (Moum & Smyth, 2019), whilst creating fundamental structure and movement within the ocean, crucially in the upper ocean layers (Mann & Lazier, 2005). Interactions of evaporation, wind shear and rainfall regulate temperatures of surface waters where plankton and microorganisms exist (Daly & Smith, 1993), whilst erosion, transportation and deposition are fundamental physical processes that underpin nutrient cycling and their availability to organisms at the lower trophic levels (Arrigo, 2004). Physical changes in the marine environment worldwide have been accompanied by notable biological changes. Long-term studies over the last century have established clear links between changes in sea temperature and biological fluctuations, whereby periods of warming and cooling have been associated with redistribution of fish, plankton, and intertidal organisms (Hawkins et al, 2003). Observed changes in distributions of top predators have been attributed to these prey distribution shifts (Gallagher et al., 2021), whilst some predator species have switched prey in response to trophic changes within their habitat (Nøttestad et al., 2015). Climate change in the marine environment is predicted to most notably affect coastal zones, where there will be increased occurrence and intensity of storm surges and upwelling, resulting in increases in rate of coastal erosion, incidences of flooding and loss of coastal regions (Pollard, et al, 2018). The North Atlantic Oscillation (NAO) climate index is derived from pressure differences at sea-level (NOAA, n.d) and is responsible for changes in the intensity and location of the North Atlantic jet stream, which have significant influence over weather and climate in the US and Europe (Met Office, n.d.). It has exhibited an increased frequency in the positive phase since 1950, marked by increased precipitation and stronger winds, is projected to continue with greater intensity (Phillips et al, 2013). This is set to be accompanied by complex alterations to distributions and prevalence of marine-life, alongside restructuring and/or loss of existing ecosystems, particularly along coastlines (Weiskopf, 2020).

Whilst seabirds rely on land in coastal areas to raise their young, this group has evolved to source and process everything they need to sustain themselves solely from the marine environment (Balance et al, 2019). As such, they spend a significant amount of their life here and have a close affinity with physical features within the marine environment, with many seabird species having developed adaptions and learned behaviours to detect and to take advantage of processes which indicate aggregations of marine prey (Tew Kai et al, 2009). Typical prey species targeted by seabirds include small fish, squid, and shrimp, but also zooplankton (Shealer, 2001). Their occurrence at different trophic levels makes seabirds useful monitors of the marine environment (Furness, 1997). Seabirds are a long-lived group of birds, and factors that affect adult survival are typically considered to have the greatest influence on population growth and decline (Searle et al., 2022). This was observed in the improved protection of birds from hunting and persecution in Britain and Ireland during the late 20th century, which contributed to notable population increases in thirteen seabird species. Other factors such as senescence, disease, reduced food availability, predation, oil spills and major storms, have also been deemed as contributors to reductions in adult survival of seabirds (Ratcliffe et al., 2004). Therefore, despite the improved hunting protections, three species of tern declined by more than 10%, due to other variables within their environment. With diverse physical and biological interactions occurring at different colony sites and variable impacts upon individual species, understanding the relative influence of each environmental factor at species level, can be invaluable for informing conservation and marine management.

Climate Change is having a broad range of effects on the marine environment; for seabirds, rising temperatures are causing shifts in breeding ranges and timings, due to the alterations in fish spawning and availability of specific prey items during the breeding period (Grémillet & Boulinier, 2009). It is also having an influence on overwintering food availability: significant reductions in zooplankton at key upwelling areas experiencing increased sea temperatures, has caused dramatic shifts in non-breeding shearwater foraging locations (Veit et al.,1996). Whilst seabirds are collectively known for their plasticity in response to environmental change and associated fluctuations in prey availability (Litzow et al., 2002), increased energy expenditure for foraging seabirds can have devastating impacts on adult survival, and subsequently overall populations long-term, if effects of climate change are sustained for successive years (Mitchell, 2006). Among seabirds, populations of arctic terns are perhaps particularly vulnerable to environmental changes. This is due to their specialised foraging strategies as surface feeders (Robertson et al., 2014; Morten et al, 2008), their dependence on areas of high marine productivity and use of global systems to support all stages of their life cycle (Hromádková et al., 2020). During the breeding season, arctic terns breed in the northern hemisphere and feed in coastal environments on small fish such as sandeel, herring and sprat (Monaghan et al.,1989). Sandeel *Ammodytes spp*. constitutes a significant proportion of the arctic tern's diet and localised reductions in stocks have been linked to poor breeding success (Uttley et al, 1989; Frederiksen et al., 2004) and overall colony declines, believed to be associated with rising sea temperatures (Arnott & Ruxton, 2002). Following the breeding season, arctic terns migrate to the southern hemisphere, via several staging areas (Redfern & Bevan, 2022) before spending a prolonged period feeding on krill around Antarctic sea- ice (Redfern & Bevan, 2019). This species is tactical in their utilisation of global wind systems to reduce energy outputs when travelling along migration routes and in their targeting of areas of high marine productivity (Egevang et al., 2010). There is evidence that surface feeding seabirds often will target upwelling systems along coastlines along key routes, with arctic terns showing strong affinity with these systems along migration (Mcknight et al., 2013). However, as coastal environments are vulnerable to environmental change, where prolonged storms along migratory routes have been known to occur, they have caused high mortality rates in seabirds through starvation, exhaustion and drowning (Morley et al., 2016). Consequently, with arctic terns being susceptible to environmental changes at the breeding and wintering grounds, an understanding of influences on their population needs to consider the different processes in the various locations.

Collectively, studies on the effects of climate conditions on tern foraging behaviour have established some links between wind speed, wind direction, sea temperatures and air temperature in relation to foraging trip lengths, frequency, and directionality, but also some minor effects from cloud cover, visibility, and precipitation (McGarrigle, 2017). A range of studies have been conducted on terns during the breeding and non-breeding periods.

Breeding Season: Tern chick provisioning studies have shown that provisioning rates have a significant influence on chick condition and survival (Wendeln & Becker, 1999), although few have investigated links between provisioning and productivity with climate. Early studies on terns found broad links between climate conditions and their effects on chick condition. Langham (1968) showed that daily weight changes in chicks of arctic terns, common terns *Sterna hirundo Linnaeus*. and roseate terns *Sterna dougallii Montagu* were affected by windspeed, duration of sunshine and amount of rainfall, with Dunn (1975) able to identify a threshold of above 15 knots of wind before common and roseate tern chicks would begin to lose weight consistently. Neither study specified however whether the weight changes were due to provisioning rates, exposure to conditions or other factors. Where links between climate and tern chick productivity have been studied directly, there have not been significant findings, thought to be due to the complex interactions that occur at breeding colonies. Recent studies at the largest colony in Europe (Morten et al., 2022) distinguished links between low food availability and poor fledgling success, and while Mallory et al (2017) could not determine independent effects of weather, they identified that low food availability and high predation pressures often co-occur in years of poor chick productivity. This was deducted from observed patterns in years with low reproduction, where there was simultaneously low adult body mass, clutch size and hatchling success, alongside high nest abandonment. As food availability and predation can be influenced by climate variables (Zhang et al., 2017), there are potentially indirect impacts of climate change occurring.

Non-breeding Season: Studies on effects of climate change on migrating arctic terns have been in development over the past decade due to the identified susceptibility of this species and advancement and wider use of tracking devices. A recent model-based study by Morten et al (2023), which used tracking and climate data alongside climate predictions, suggested that foraging arctic terns on migration may be affected by climate change but only at the north Atlantic gyre where net primary productivity is likely to decline. Minor impacts at other key feeding areas are predicted during the non-breeding season which individually are not enough to impact tern survival, however given the large spatial ranges terns travel, these may have a greater cumulative impact on the birds during the entire non-breeding period. Whilst the study found that climate change may affect foraging terns and acknowledges from other studies that reduced foraging ability can increase tern mortality, it does not link this to any population data to evaluate the real time effects on tern survival. Studies either examine observed population changes and survival rates (Mallory et al., 2018), or focus on climate trends which may affect artic tern foraging (Morten et al., 2023), but there is an absence of studies examining how climate variables affect overwinter survival rates or how they may impact terns quantitatively at the population level. However, Redfern and Bevans' tracking study in 2019, presented some valuable insight into how future studies on this topic could be approached. Whilst it provided further evidence on the affinity of arctic terns with sea ice and the distinct influence of its extent and distribution on their movements, it was not able to conclude that arctic terns will be affected by reductions in sea ice in West Antarctica, due to the observed increases in the Ross Sea and East Antarctica (Parkinson & Cavalieri, 2012). It overall empahasised the importance of monitoring this species' responses to long- and short-term changes in sea ice extent and ultimately their ability to adapt.

What is becoming more apparent is both the variability of conditions and degrees of environmental change experienced by seabirds at different colony sites and along their migration routes. There is evidence to suggest that demographic changes due to climate change can occur at small and large spatial scales; arctic tern colonies are exhibiting variability in population trends within the UK and internationally and could be a species where behavioural and geographical differences are contributing to mixed effects from climate change. There is a need for studies looking across the annual cycle, as well as combining short-term behavioural studies with long-term population studies.

Given the encroachment of climate change effects into areas where arctic terns both breed and overwinter, it is important to establish the sensitivity and adaptability of this species to climatic variables which are exhibiting patterns of long-term change, so that any potential consequences on seabirds may be predicted for the future as climate trends progress. Whilst all arctic terns migrate to the southern hemisphere and face similar conditions each year, due to the different biological pressures and human induced factors at different colonies, as well as geographical influences on foraging areas and migratory timings, it is necessary to assess population change at individual colonies, particularly considering the affinity these birds often show to where they are born. Changes in the intensity and frequency of storms can impact foraging terns by hampering flight and dive performance. These increased energetic demands and reducing foraging success could impact populations through reduced chick provisioning rates in breeding seasons or survival rates in non-breeding seasons (Thorne et al., 2023). To investigate some of the effects of climatic variables on seabird demographics, three hypotheses were tested on a single arctic tern colony:

H_1: Regional climate conditions at breeding, migratory and overwinter feeding areas have a significant influence on adult survival.

H_2: Regional climate conditions at breeding, migratory and overwinter feeding areas have a significant influence on arctic tern chick productivity.

H_3: Local climate conditions have significant influence on the probability of chick provisioning.

2 Methods

2.1 Study Site

The Skerries are a group of sparsely vegetated rocky islets approximately 17 ha in extent, located 3Km northwest of mainland Anglesey in Wales, UK (NRW, 2015). They form part of the Anglesey Tern Colonies SPA, which in the spring and summer months support important UK populations of breeding tern species. In 2022, The Skerries supported arctic tern (2930 pairs), common tern (350 pairs), roseate tern (1 pair), alongside other coastal breeding species such as Atlantic puffin *Fratercula arctica* (741 AOB[1]), great black-backed gull *Larus marinus* (38 pairs) and lesser black-backed gull *Larus fuscus* (122 pairs). Cemlyn Bay located 6km East Southeast on mainland Anglesey (see Figure 1), also forms part of this SPA and hosts sandwich tern *Thalasseus sandvicensis* (2400 AON[2]), arctic tern (206 AON) and common tern (150 AON), (BTO, 2022).

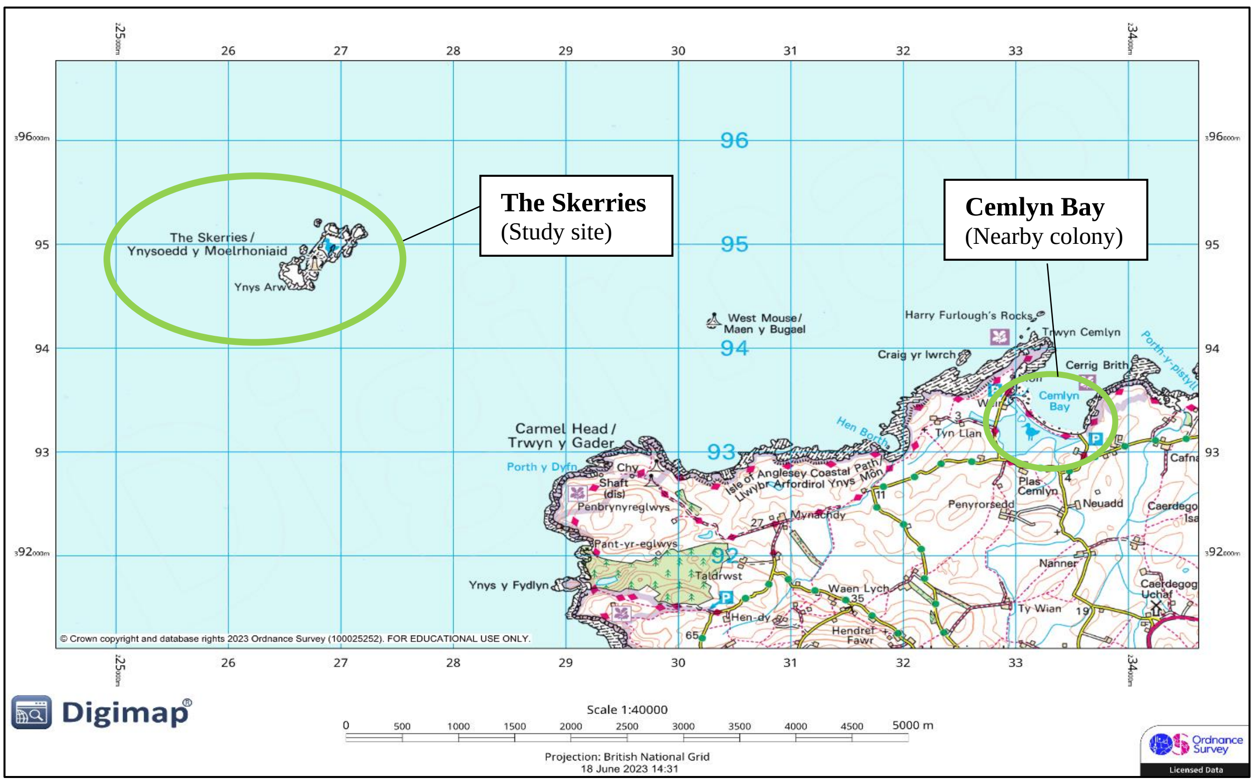

Figure 1. *OS Map of the study site location, The Skerries, and the neighbouring colony at Cemlyn Bay on Anglesey, North Wales.*

[1] AOB – Apparently occupied burrow
[2] AON- Apparently occupied nest

2.2 Data Collection

2.2.1 *Overview*

This project first utilised long-term productivity and ringing data provided by RSPB to test whether annual variation and any long-term changes in adult survival and productivity could be explained by regional environmental conditions both during, and outside of the breeding season. Firstly, long-term monitoring data from the RSPB was supplemented with meteorological data from climate indices, quantifying environmental conditions across the study regions and periods. Secondly, to identify a potential mechanistic link between foraging success and oceanographic conditions out at sea, a provisioning study was conducted during the 2022 breeding season, to investigate if local environmental conditions were having a significant influence on tern foraging ability and assess whether climate trends could explain changes in population dynamics in terms of adult survival and productivity of arctic terns.

2.2.2 *Long-term study*

Climate Index Data

To account for the transient life cycle of the arctic tern, which involves utilisation of numerous feeding areas in both the northern and southern hemispheres each year, and absence of colony-specific migration information, climate indexes were used to detect any broad scale patterns in productivity and adult survival associated with conditions along migration and wintering periods as well as during the breeding season for comparison. Two datasets, the North Atlantic Oscillation (NAO) and Southern Annular Mode (SAM) were gathered from the National Oceanic and Atmospheric Association (NOAA) online databases. The latter is indicative of conditions in the southern wintering area, whereas the former is indicative of conditions in the northern breeding area. The data was available at monthly intervals and only data from 1986-2022 was selected, to correspond with when consistent data on arctic tern populations and productivity began to be collected on The Skerries, Anglesey. The data was separated into time intervals (see Table 1) corresponding with relative times UK and Dutch arctic terns have been reported in each hemisphere along north and south migrations, breeding and in overwinter feeding areas (Redfern & Bevan, 2022; Fijn et al., 2013).

Table 1. *Climate indexes at arctic tern locations during different stages of their annual life cycle.*

Reference	Time Period	Index	Months	Tern Locations
SAMAS	Antarctic summer	SAM	Dec-Feb	Antarctica, Weddell Sea
NAONM	North Migration	NAO	Mar-Apr	ACZ, North Atlantic, Irish Sea
NAONH	Northern Hemisphere	NAO	Apr-Aug	N Atlantic, Irish Sea, Wales
NAOBR	Breeding	NAO	May-July	Wales, Irish Sea
NAOSM	South Migration	NAO	Aug-Sept	Irish Sea, ACZ
SAMSM	South Migration	SAM	Aug-Sept	ACZ, W. Africa, S. Africa
SAMNB	Non-Breeding	SAM	Oct-Mar	ACZ, W. Africa, Indian Ocean, Antarctica

Adult ringing data

Adult-ringing data was sourced from an RSPB leg flagging project initiated in 2013 by Steve Dodd, aimed at studying adult survival of common and arctic terns within the Anglesey Terns SPA. Leg flags have been deployed at the skerries tern colony every year until 2022, except for 2020 when the colony was abandoned by the terns. A summary of the number of flags deployed annually during this 10-year period is provided in Table 2. The flags are vivid yellow, with two letter codes printed in black to allow the code to be read from a distance, i.e through optics such as binoculars or telescopes, or by eyesight at short range. Letter codes are individual to each bird and correspond to a standard British Trust for Ornithology (BTO) metal ring information held on a national database, taken at time of ringing. Information primarily includes location, weight, wing length, relative age, and presence of a brood patch to indicate if breeding adult. Given the vast number of birds on the island, the scheme aims to allow for easier and less invasive monitoring of tagged birds, as wardens periodically scan for them within the colony over the entire breeding season, theoretically enabling a higher 'recapture' rate. Only incubating adults on nests have been given yellow leg flags, ensuring the entire dataset contains only data on birds which have survived at least two-three winters prior to capture and are at breeding age (BTO, 2015). This is beneficial to later analysis as it reduces the influences that inherent high mortality and later arrival of immature birds have on re-sighting (Langham, 1971; Riotte-Lambert & Weimerskirch, 2013; Dittmann & Becker, 2003).

Table 2. Annual numbers of new flags deployed and flags either re-trapped or re-sighted.

	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Total
New Flags	50	49	30	19	23	5	9	0	36	19	240
Re-traps + Re-sightings	35	51	78	127	65	102	90	N/A	60	51	659
Re-traps including duplicates	53	67	253	308	130	367	308	N/A	163	212	1861

Adult survival estimates were run in the program MARK (White & Burnham, 1999) using live recapture data. This program, available at phidot.org, is a widely used software application for the analysis of data from marked individuals. The analysis allowed both the probability of resighting (p) and survival (Phi) to vary with time (t). Based on the AIC output, the Sin link function was selected to run the model: {Phi(t)p(t)}. There were 9 encounter occasions and 8 intervals input into the model, then time intervals set at 1 year for all intervals except the 7th interval between 2019 and 2021 where 2 years was entered i.e. 11111121.

Productivity

RSPB wardens have collected productivity data on the skerries in all years from 1989 to 2022, except for 2007 and 2020 where there were no wardens on the island. Tern productivity on the site is determined by a combination of strategies; subtraction of all observed and found losses since the principal clutch count, extrapolation of study nest outcomes, and final fledgling counts (RSPB 2021). Productivity is measured as number of chicks fledged per pair which is calculated by comparing the number of adult pairs incubating eggs at the onset of the season in study nests, against a fledgling count towards the end of the season when most chicks are over 15 days old and either recently or nearly fledged.

2.2.3 *Short-term study*

<u>Camera Trap Data</u>

Four browning Recon Force Edge trail cameras were deployed within arctic tern nesting enclosures in late May 2022 during incubation period for the colony. Successive deployments were made at, on average, variable intervals between 4 and 15 days (see Table 3), depending on weather conditions and accessibility to the island. These were existing enclosures which were previously set up by the wardens for their long-term monitoring studies. These cameras had a 0.2s trigger speed and were set to record 20 second videos at 1920 × 1080 resolution (HD) and 30fps, with a 15 second interval. An additional five Bushnell Trophy Cam Aggressor HD trail cameras were also deployed at different positions in the pens to provide backup footage should any technical faults occur, time stamps need checking, or confirm provisioning events. These cameras also took 20 second videos with 15 second interval, however these had a 0.6s trigger speed and recorded videos at 1280 x 720 resolution and 30fps. All data was routinely transferred onto external hard drives and organised according to deployment, enclosure and nest ID. Provisioning events were noted in videos by recording each time an adult brought a fish back to the nest for the chick. Instances where terns brought back fish for partners were recorded separately and did not form the analysis of provisioning data.

Once collated, only nests which had more than 15 provisions on at least one deployment and 3 or more days of provisioning in total, to rule out any nests which may not have been reliably triggered by cameras; out of 14 nests that the cameras covered, 8 were used in analysis. Cameras typically covered multiple nests with varying success between deployments therefore a summary of trail camera data used in the analysis is presented by nest number and deployment in Table 4. During data processing, each hours was populated as either having presence (1) or absence (0) of a provisioning event, and then proportion of hours with provisioning events for each nest was calculated, to give a probability of provisioning, which is presented in Table 5.

Table 3. *Trail camera deployment summary.*

	Dep 1	**Dep 2**	**Dep 3**	**Dep 4**	**Dep 5**
Dep date	28-May	6-Jun	16-Jun	20-Jun	5-Jul
Dep time	11:00	11:00	12:00	14:30	11:30
Eggs	Y	Y	Y	N	N
Chicks	N	Y	Y	Y	Y

Table 4. *Summary of trail camera data used in the analysis.*

Nest ID	**Deployment**	**Start**	**End**
47	2	12/06/2022 11:03	14/06/2022 10:33

19	3	16/06/2022 14:22	20/06/2022 14:51
20	3	16/06/2022 14:22	20/06/2022 14:51
21	3	16/06/2022 12:38	18/06/2022 14:33
46	3	16/06/2022 14:14	20/06/2022 06:54
47	3	16/06/2022 14:18	18/06/2022 05:12
16	4	20/06/2022 14:30	21/06/2022 08:01
47	4	20/06/2022 14:38	29/06/2022 05:54
10	5	05/07/2022 11:57	07/07/2022 07:12
16	5	05/07/2022 11:57	07/07/2022 07:12
18	5	05/07/2022 12:16	07/07/2022 15:27
19	5	05/07/2022 12:16	07/07/2022 15:27
20	5	05/07/2022 12:16	07/07/2022 15:27
21	5	05/07/2022 12:16	07/07/2022 15:27
47	5	05/07/2022 12:52	08/07/2022 12:26

Table 5. *Proportion of hours with provisioning events for each nest.*

Nest ID	**Proportion**
10	0.267
16	0.312
18	0.327
19	0.262
20	0.188
21	0.388
46	0.124
47	0.185

2.2.4 *Environmental Data*

ERA5

Local climate data from the Copernicus ERA5 online data was used to compare with 2022 provisioning data collected for this study. This is a compilation of European climate data from a meteorological model including land, atmospheric and oceanic variables provided by the EU's space program. The dataset is derived from a combination of observational data from satellites and ground sensors; it is scientifically validated and used extensively in research and forecasting. Local data pertaining to a $5km^2$ area immediately around The Skerries, Anglesey was extracted at (N 53.50, E -4.3, S 53.30, W -4.8) at hourly intervals, which was assessed as sufficient to detect the level of change required for this study. The terns are likely feeding along west and north Anglesey, which is suspectable to local-scale variations in weather conditions. The positioning of a weather station would be susceptible to these local variations, however the modelled data allowed conditions to be amalgamated over a potential foraging range and were sufficient to discriminate amongst weather events in this study. Using model-derived data also allowed scope for collecting detailed information on both oceanic and atmospheric conditions, which presented additional variables for statistical testing that a land-based weather station would not provide. Specific variables extracted were sea-surface temperature, wave height, rainfall and cloud cover. The data period selected covered the core chick rearing period for this colony; the first chick hatched on the 12th of June, so only data for June and July was used.

Tidal

Local tidal data was sourced from WXTide32 database for use in the analysis with provisioning and ERA5 climate data during the 2022 arctic tern breeding season. Data from the nearest tidal current station to the skerries, Amlwch Port was used, located approximately 18km ESE. Data covered the chick rearing period between June and July 2022.

2.3 Analysis

2.3.1 *Data Processing*

Time was divided into 1hr intervals, and the presence (1) or absence (0) of provisioning activities within each hour was obtained. Therefore, if a chick was provisioned multiple times in 1 hour, this would be represented by a 1 rather than the number of provisioning events. This approach was taken because: (a) the interest was in broad-level changes in provisioning activities across cycles (tide and diurnal) and days (weather) rather than provisioning rates *per se* (b) processing at smaller intervals (i.e. minutes) then high zero-inflation would reduce likelihood of detecting patterns, would culminate in pseudo-replications and temporal autocorrelation, (c) using provisioning rates would produce overdispersion with many zeros and occasional high-counts.

2.3.2 *Provisioning and Local Climate*

The 2022 provisioning data collected for this study was analysed using a generalised additive mixed model (GAMM) with a binomial distribution in RStudio. Data were processed into hourly intervals, with the presence (1) or absence (0) of provisioning obtained for each hour, before being combined with concurrent environmental data. Six ERA5 meteorological conditions (see section 2.21) and tidal depth (m) were used as fixed explanatory variables and presence (1) or absence (0) of provisioning used as the response variable. All explanatory variables were included, and backwards model selection (Table 6) was used to identify statistically significant relationships ($p<0.05$). Nest ID was used as a random explanatory variable, to identify which explanatory variable had the most influence on probability of provisioning. Random effects between different nests were included to account for differences in probability of provisioning amongst nests (see Table 5) that would not be due to climate conditions, such as age of chick, parent body condition, breeding experience, or differences in predation rate between enclosure locations. This allowed the relative influence of environmental conditions on provisioning within nests to be investigated. Random effects were selected over fixed effects because multiple nests were studied, and including the latter would increase degrees of freedom and decrease statistical power to detect relationships with environmental conditions. Following model construction, the probability of a provisioning event per hour was estimated across environmental gradients and cycles. In these estimations, Nest 19 was used because this represented the median probability of provisioning amongst all nests.

Table 6. *Significant factors identified through backwards model selection.*

	edf	**Ref.df**	**Chi.sq**	**p-value**
Time of Day (decimal day)	3.983	4.000	82.512	<0.001
Julian Date	1.457	1.700	22.906	<0.001
Wave Height (m)	1.874	1.978	9.736	0.0090
Nest ID	3.972	7.000	10.137	0.0142

2.3.3 *Climate Indexes and Demography*

NOA and SAM data were analysed against the long-term productivity and adult survival data in RStudio to examine whether any relationships exist between climate patterns and demographic variation between years (productivity and adult survival). As productivity and adult survival data had a gaussian and binomial distribution, linear and generalized linear models were used, respectively.

3 Results

3.1 *Survival*

Survival analysis in MARK indicates that between 2013 and 2022, adult survival of arctic terns has overall declined on the skerries Anglesey (Figure 2). Initial annual survival rates averaged above 0.9 until 2017. They rose again to similar levels in 2018 but have shown an overall decline in the four-year period since this time with latest survival estimates at 0.65.

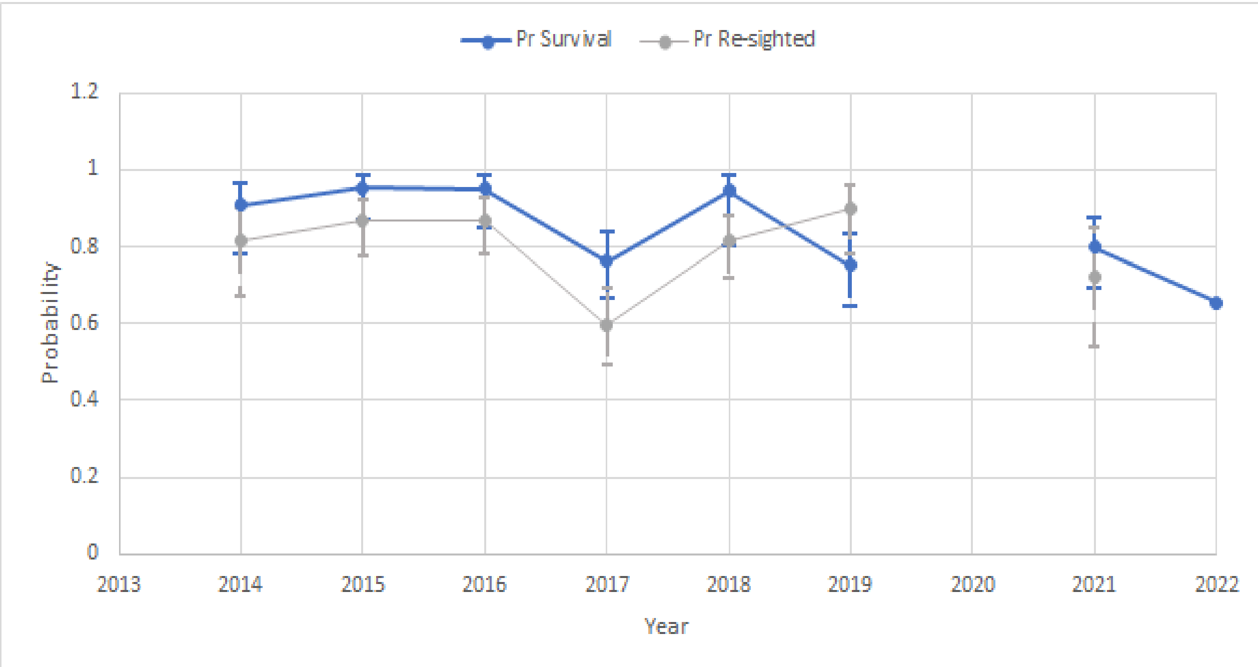

Figure 2. *Estimated probabilities (Pr) of adult arctic tern survival and re-sighting on the Skerries, Anglesey between 2013 and 2022. The year 2020 has no data due to colony abandonment following peregrine activity.*

No significant relationships could be identified between NAO and SAM indexes and annual adult survival. Table 7. presents the statistical results and figure 3 shows large variability in adult survival across a range of NAO and SAM time series. See Table 1 for details on each time period.

Table 7. Statistical outputs for NAO and SAM during different life stages when compared with annual adult survival.

Time period	**Estimate**	**Std error**	**p-value**
NAONM	0.022	0.088	0.810
SAMAS	0.015	0.067	0.839
NAOSM	-0.041	0.049	0.438
SAMSM	-0.033	0.049	0.528
NAOBR	0.006	0.047	0.911
SAMNB	-0.009	0.087	0.917

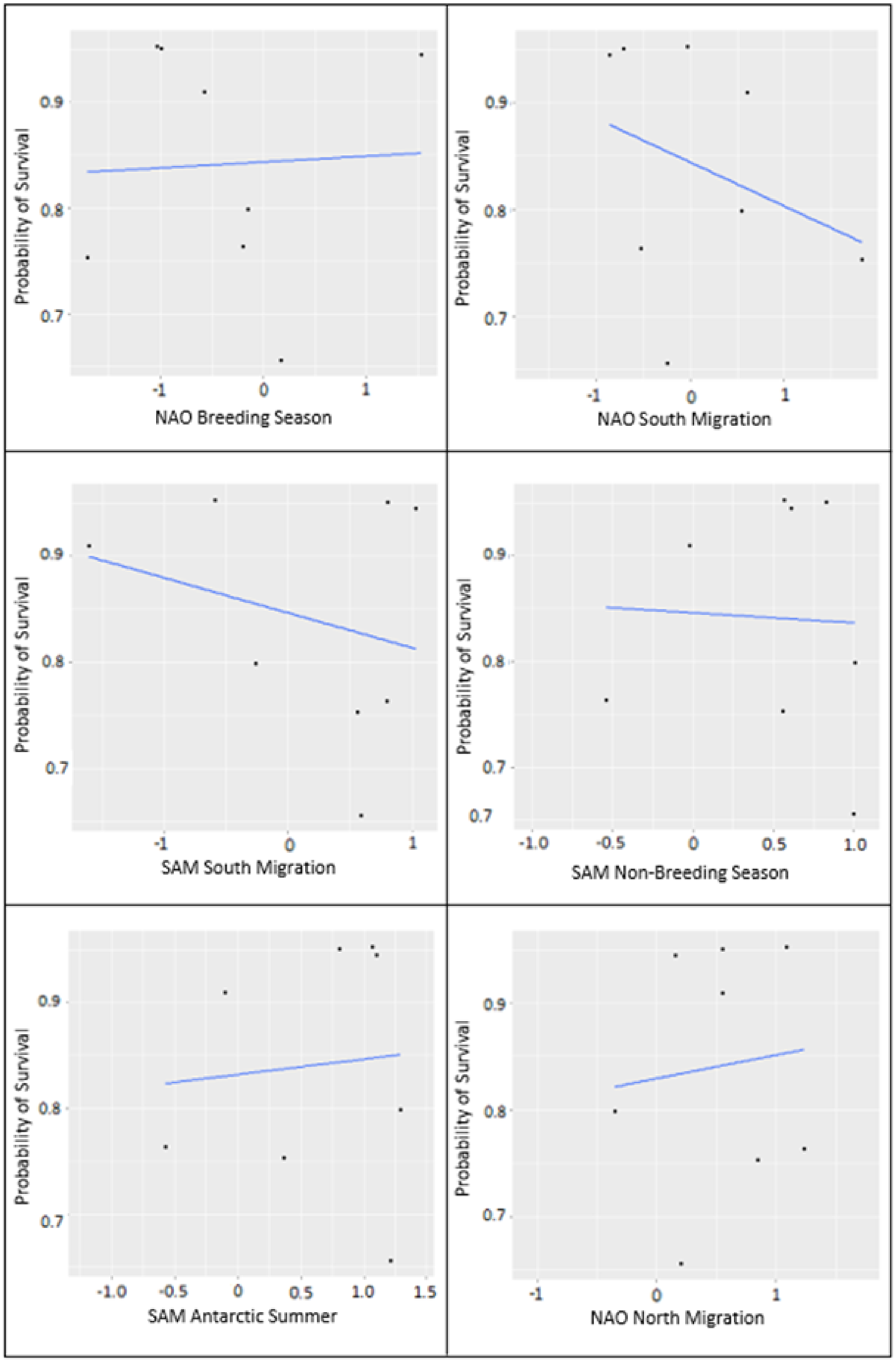

Figure 3*. NAO and SAM values at different periods of annual life cycle compared with adult survival.*

3.2 *Productivity*

A non-significant negative relationship (p=0.077, F=3.374) was observed between the NAO index during the northern migration (March- April) immediately prior to the breeding season and productivity of arctic terns in that subsequent breeding season.

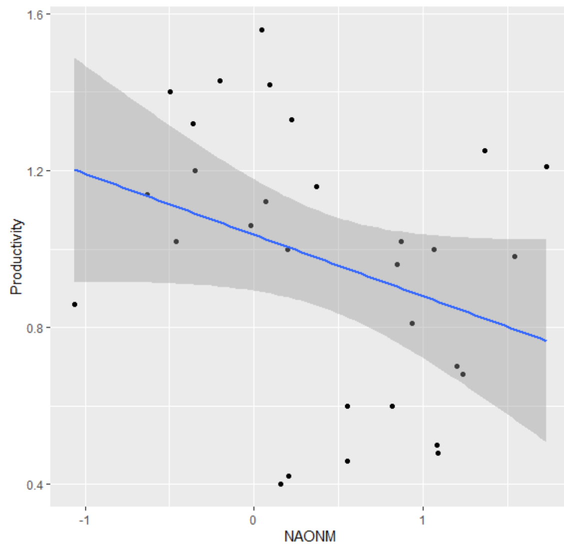

Figure 4. *Annual productivity of the Skerries Arctic terns compared to NAO during their north migration prior to the breeding season (NAONM).*

A non-significant negative relationship (p=0.584, F=0.307) was observed between the NAO index during the arctic terns' core breeding months (May-July) and productivity of arctic terns in that respective breeding season.

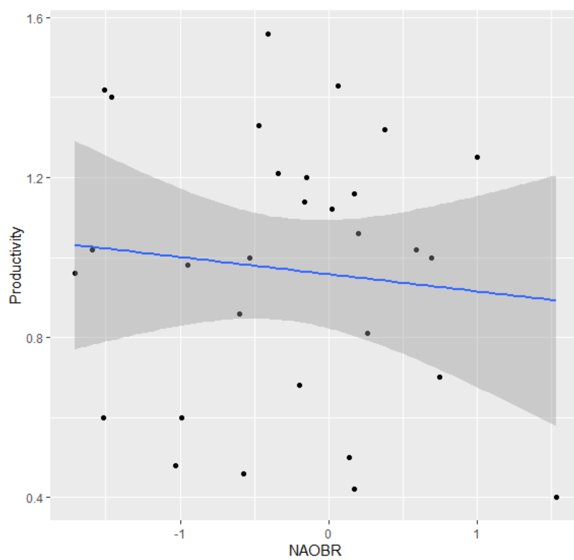

Figure 5. *Annual productivity of the Skerries Arctic terns compared to NAO during their breeding season (NAOBR).*

A non-significant negative relationship (p=0.425, F=0.656) was observed between the SAM index while arctic terns are in the non-breeding season (October-March) and productivity of arctic terns in the following breeding season.

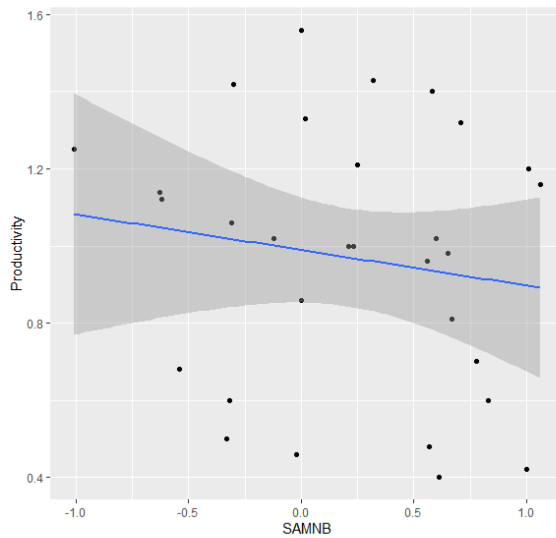

Figure 6. *Annual productivity of the Skerries Arctic terns compared to SAM during their non-breeding period, prior to the breeding season (SAMNB).*

A non-significant negative relationship (p=0.466, F=0.547) was observed between the NAO index while arctic terns are in the northern hemisphere (April- August) and productivity of arctic terns in that respective breeding season.

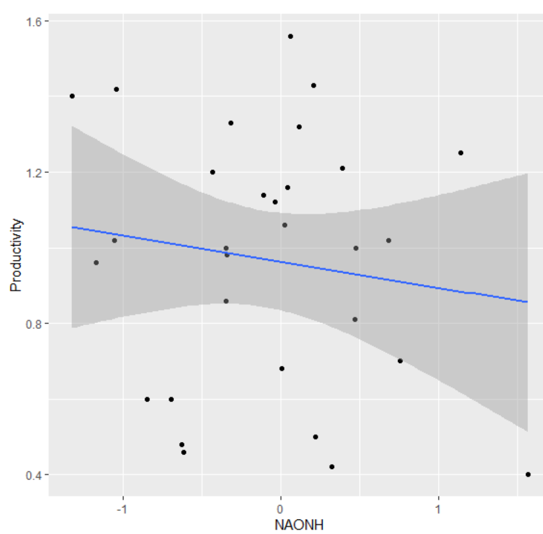

Figure 7. *Annual productivity of the Skerries Arctic terns compared to NAO when they are in the northern hemisphere prior to, during and immediately after the breeding season (NAONH).*

Provisioning

Wave height had a significant effect on probability of provisioning, whereby the probability of provisioning per hour significantly increased with wave height between 0-0.8m and significantly reduced with subsequently higher wave heights, (n= 1023, chi-squared = 9.736, p= 0.0090). During the 2022 arctic tern breeding season, the estimated probability of provisioning per hour varied between 0.03 and 0.26 when compared with wave height (Figure 8). Wave heights of 1.5m had equal provisioning probability (0.17) to when there are no waves (0m). Above 1.5m wave heights there was a continued negative effect on provisioning whereby probability of provisioning per hour reached lows of 0.03 at wave heights of 2.5m. Other variables such as rainfall, sea surface temperature and cloud cover did not show any significant influence on chick provisioning.

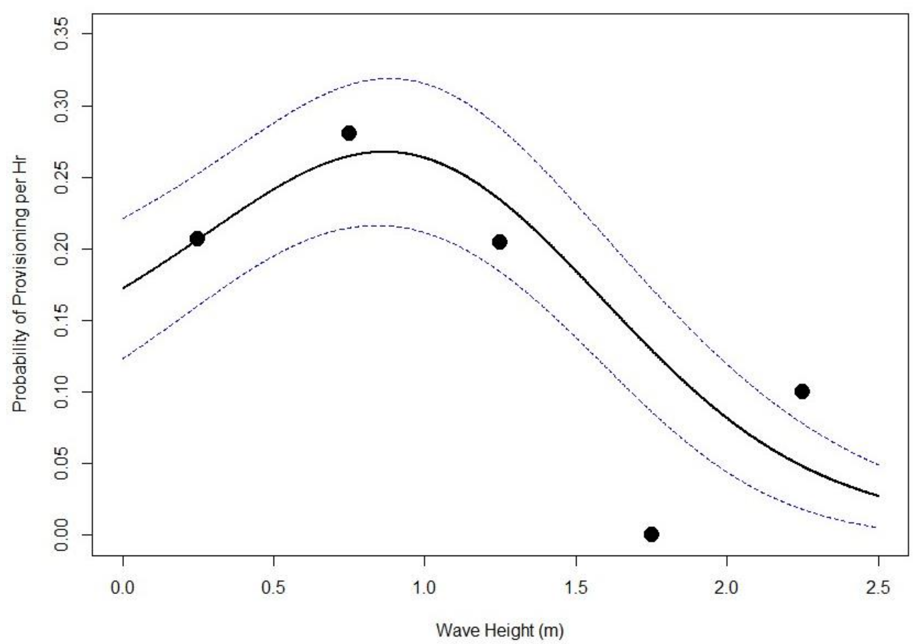

Figure 8. *The probability of an Arctic tern parent provisioning its chick per hour during variable wave heights (m) around the skerries, Anglesey in June and July 2022.*

Through the model section process, time of day was additionally identified as having a significant influence on chick provisioning, (n=1023, chi squared =82.512, <0.001). Figure 9 below shows the probability of chick provisioning peaking twice during the day, first mid-morning (Pr =0.43) and then again mid to late afternoon (Pr =0.48), reducing by approximately half (Pr =0.24), immediately prior to midday. Provisioning occurred at dusk and dawn but very infrequently.

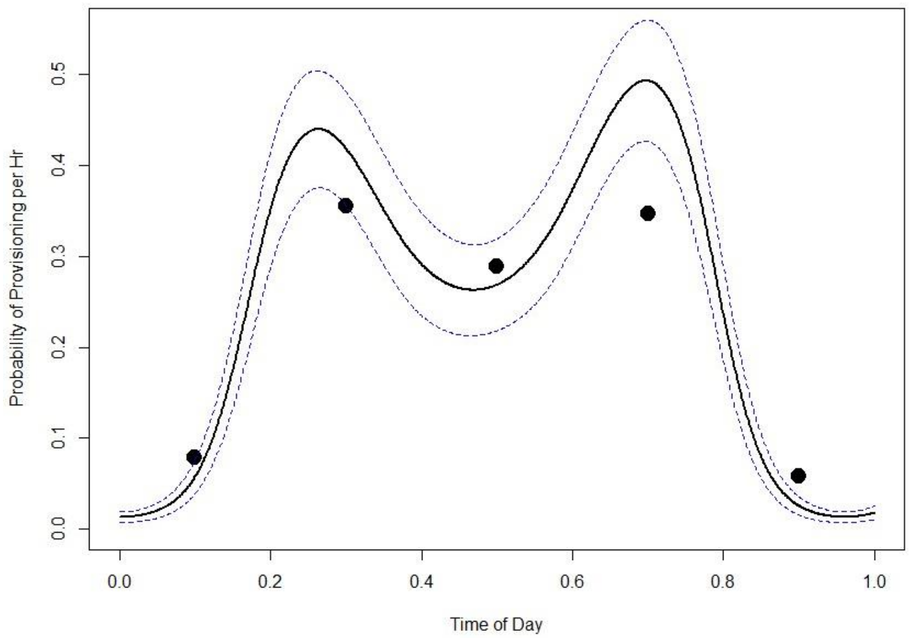

Figure 9. *The probability of an arctic tern parent provisioning its chick at different times of the day (decimal day) on the skerries, Anglesey during June and July 2022.*

4 Discussion

4.1 Summary

Regional climate conditions at breeding, migratory and overwinter feeding areas did not significantly influence adult survival. However, there was some indication that climate conditions in the northern hemisphere, when arctic terns are migrating north and stopping at pre-breeding staging areas in the North Atlantic, may have an influence on chick productivity at the colony in the successive breeding season. Additionally, wave height around the skerries, was shown to significantly influence chick provisioning at the breeding colony alongside time of day. These results will be considered separately before being combined when assessing potential impacts of environmental change on this population.

4.2 *Survival*

No relationships between adult survival of the skerries arctic terns and regional climate patterns were found during analysis. Whilst the effects of weather and climate have been documented as influencing adult survival in terns and other seabirds (Frederiksen et al., 2008; Schreiber, 2001), the survival rates of this arctic tern colony have not been adversely influenced by weather conditions over the past decade, despite variability in NAO and SAM. Similar findings from a study on puffins where extreme weather was not a driving factor behind observed patterns in adult survival, and were instead attributed to bottom-up trophic interactions (Reiertsen et al, 2021). This highlights the need to examine indirect and lagged effects of climate variability and their impacts on lower trophic organisms within food webs where terns are top predators. Consideration of biological factors during their lifecycle that may have greater or sufficiently significant effects on adult survival is also needed. Common factors reported at arctic tern colonies affecting mortality are disease and predation (Scopel & Diamond 2017; Redfern et al, 2020), which have both been confirmed on the skerries in recent years (Grozelier & Nunnerley, 2021). The highly pathogenic avian influenza (HPAI) outbreak in 2022 particularly demonstrated the devastating consequences disease can have on tern colonies (Knief et al., 2024). However, the increasing distances of tern breeding dispersal observed over the past several decades (Møller et al, 2006) adds another element of complexity to interpretation of survival data, as they could account for lower than expected and sporadic re-sighting rates.

Synchronicity in rates of tag deployment and adult survival indicate the wide variation in tag quantities deployed each year, was having a strong influence on the number of re-sightings in successive years, in turn skewing survival rates. Variation in survey effort for re-sightings themselves may also have had an influence, as it is a limitation often faced by seabird re-capture studies (Horswill et al., 2016). The exact age of adult birds at tagging is also unknown, allowing for great variability in initial ages and ordinary lifespan remaining. These scenarios alongside small sample sizes within a large multi-species colony, could have presented difficulties in achieving representative and comparable re-sighting levels. A final but important consideration during analysis was the use of large-scale climate indices such as NAO and SAM, which are potentially too broad to capture local conditions experienced by the terns, given their wide-ranging dispersal over the non- breeding period. On review of the limitations presented by the methodology, a longer-time series together with larger and consistent sample sizes, and more precise knowledge of this colonies' wintering areas are needed to confidently assess any effects of climate conditions on survival of these birds.

4.3 *Productivity*

No significant relationships between annual productivity and regional climate patterns were found during analysis. However, a near significant result ($p=0.077$) was found between the climate conditions in the northern hemisphere immediately prior to the arctic terns' return to the breeding colony, and their successive productivity for that year. This gives some indication that pre-breeding feeding areas in the North Atlantic are important for the breeding success of this arctic tern colony. These are likely to be in areas within and stemming from the OSPAR region which has been identified as an area of high marine productivity and seabird biodiversity hotspot (Davies et al., 2021). The relationship observed corresponds with what is known about carry-over effects of winter body mass exhibited in seabirds (Salton et al., 2015) whereby higher winter body mass typically corresponds to earlier and more successful breeding. Additionally, there is potential for the occurrence of lagged impacts, whereby pre-breeding climate conditions may enhance prey abundance in breeding grounds before arrival of the colony, providing better support to the birds through the breeding season. Such effects have previously been observed on breeding kittiwakes where winter sea-temperatures one year prior at the breeding grounds, were negatively correlated with breeding success (Frederiksen et al, 2007). This result whilst not significant, indicates possible value in identifying the precise locations of this colonies' pre-breeding staging areas in the North Atlantic, so that the relationship with local climate conditions there with subsequent breeding success. More broadly, it highlights the need to consider indirect relationships between environmental conditions outside breeding season and breeding success of arctic terns.

4.4 *Provisioning*

Wave height and time of day both had significant effects on probability of provisioning. Moderate waves were found to enable arctic terns to provision their chicks more regularly than when there were no waves or tall waves. Moreover, very tall waves had a significantly negative impact on terns' ability to provision their chicks. With arctic terns being surface feeders that are restricted to the first 50cm of the surface (Morten et al, 2022), it is possible that no waves and tall waves both negatively impacts terns' ability to forage effectively. There are potentially combined effects from reduced ability of terns to detect *and* access prey in these conditions due to the physical changes in the water and prey responses to these changes. In terms of detection, reduced visibility and increased cognitive processing demands for foraging terns during conditions with tall waves, have been known to reduce the frequency of their foraging attempts (Taylor, 1983). However, the influence of fish adjusting their position in the water column in response to wave shading, contributes further to prevent predator detection (Kaartvedt et al 2012). If fish move lower and become less detectable in both calm and very wavy conditions, respectively, moderate waves are likely optimal for arctic tern foraging, due to the increased availability of fish near the surface, and subsequently increased ability of terns to detect prey.

Beyond predator detection prevention, fish positioning in the water column is also driven by distributions and abundance of plankton which they feed on. Diel vertical migrations of fish in search of plankton where they descend deeper as light availability increases during the daytime (Elliott & Gaston, 2015), may explain why there is also a significant effect from time of day on provisioning of tern chicks. Deep diving seabirds are known to dive deeper during the middle of the day because the fish descend lower and there is the most available light (Shoji et al., 2015), however arctic terns have a shallower dive depth limit which could explain the slight decrease in provisioning in the middle of the day. As the highest arctic tern provisioning rates were in the early morning and late afternoon periods, this would coincide with when plankton and fish are closer to the surface, and reduced provisioning levels in the middle of the day would coincide with when plankton and fish are typically at their lowest.

There is the possibility that lack of data at either extreme values for wave height could have contributed to the pattern observed; for example, if the conditions were rarely calm or very rough on the days the cameras were operational during the season. Given the short chick rearing period and relatively small sample size, a future study should consider obtaining a larger sample size, which could easily be achievable through different camera setups (Fijn et al., 2024). This would add confidence to the findings if the data had more samples from a broader spectrum of conditions.

The findings in relation to wave height and time of day effects on tern provisioning, highlight the importance of considering non-linear responses to physical environmental changes and identifying optimal values for seabird foraging studies.

4.5 *Conclusion*

Arctic tern populations could be vulnerable to the effects of climate change, owing to their niche as surface feeders and the anticipated effects regional and local changes in weather will have on prey behaviour, abundance and availability. Their reduced ability to forage in conditions with tall waves could make them susceptible to predicted increases in storm intensity and frequency. In the breeding season when foraging range is restricted, they could be particularly vulnerable, with subsequent impacts on chick provisioning rates and annual productivity. There is also some indication that pre-breeding climate conditions in the northern hemisphere are important to the arctic tern population, due to the impact they can have on productivity, however more detailed information is needed on the spatial and temporal usage patterns of the study colony in their wintering and migratory areas.

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