

School of Biosciences



BI3001 FINAL YEAR PROJECT REPORT 2023-24

TITLE: Chick growth and success: a product of optimal climatic conditions or parental effort? A case study on the European Storm-petrel *Hydrobates pelagicus* in Nólsoy, Faroe Islands.

STUDENT NUMBER: 1923053

DEGREE: Zoology with Preliminary Year (BSc)

TYPE OF PROJECT: Practical Project (data analysis)

WORD COUNT* (Summary): 391

WORD COUNT* (Main Body): 5533

If your project has School Research Ethics Committee approval, please cite the project number here:

Summary

Background

Monitoring climate's impacts on the growth and success of seabird chicks is not thoroughly understood but is extremely important to assess how population viability may change in the future and allow informed conservation measures to be implemented. The European Storm-petrel is the smallest Atlantic seabird and is widely distributed with the largest breeding populations situated in the Faroe Islands. This study aimed to determine whether climate has a direct or an indirect impact on chick growth, via parental provisioning, in addition to examining the overall differences in breeding success between years in a *H. pelagicus* colony in Nólsoy, Faroe Islands.

Methods

Data was collected across 2022 and 2023 in Nólsoy, Faroe Islands. Internal nest footage allowed observations of parental provisioning behaviours to be recorded. Additional data on chick weights throughout the season, hatching and fledging dates and weather data were used for analysis. Effects of climate on chick weight and parental provisioning were examined using GLMs. Differences in breeding success between each year were tested using Chi-squared and Fisher's Exact tests ($p < 0.05$).

Results

Fledging success was significantly higher in 2023 than in 2022, although no significant differences in weight between years were observed. Chicks born later in the year weighed significantly less than those born earlier in the season. Mean wind speed (m/s) and precipitation occurrence had nonsignificant associations with chick weight across all ages but mean daily temperature ($^{\circ}\text{C}$) was significantly positively associated with chick weight. Only feeding rate per hour and duration of a single feed were significantly correlated with precipitation occurrence, with feeding rate declining and feed duration increasing with rain. Significant negative associations were found between chick weight and the proportion of time a chick was brooded or unattended.

Conclusions

This study showed that climate does affect chick growth, both directly and indirectly, through the effects of temperature, wind speed and precipitation occurrence. However, relationships between climate, parental care and chick growth are multifaceted and complex. The NAO is potentially linked to overall breeding success, but further investigation is required to confirm this relationship. Accounting for other variables in further studies, such as parental age and pre-breeding season

weather, may help clarify relationships. Finally, this study may highlight how artificial nest boxes may act as a successful buffer against climatic variation.

Key terms

Climate change, behavioural plasticity, artificial nest boxes, North Atlantic Oscillation, breeding success.

Acknowledgements

I would like to thank my supervisor, Rob Thomas, and Ben Porter for their support in this project. I am very grateful to Jens-kjeld Jensen on Nólsoy for making the data collection possible through the installation of the study nest boxes in the colony, and for the support of Hannah Hereward in the use of the in-nest cameras.

Contents

SUMMARY	2
ACKNOWLEDGEMENTS	3
BACKGROUND AND AIMS	5
<i>RESEARCH QUESTIONS:</i>	8
METHODOLOGY	8
STUDY SITE	8
FIELD WORK.....	10
WEATHER DATA	10
VIDEO ANALYSIS.....	11
DATA ANALYSIS	12
RESULTS	14
SUMMARY OF TRENDS	14
INTER-ANNUAL AND DAILY DIFFERENCES.....	16
CLIMATE AND CHICK GROWTH.....	16
CLIMATE AND PARENTAL CARE.....	17
PARENTAL CARE AND CHICK GROWTH	18
DISCUSSION	20
OVERALL SUCCESS	20
CLIMATE AND CHICK GROWTH.....	21
CLIMATE, PARENTAL CARE AND CHICK GROWTH	23
CONCLUSIONS AND FUTURE DIRECTIONS	24
REFERENCES	24
APPENDIX	29

Background and aims

Seabirds are considered indicators of marine ecosystem health due to their important role as apex predators (Diamond and Devlin 2003; Parsons et al. 2008). As migratory species they spend a huge amount of time at sea, but breed in colonies on isolated land masses, such as small islands (Furness 2012), which provide more accessible opportunities to study their ecology. Seabirds feed on a variety of marine organisms, including zooplankton and large fish, using varied strategies, such as water diving (Oro and Martínez-Abraín 2009). Often, their migratory nature makes them particularly vulnerable to changing environments, including anthropogenic pressures. Like other migratory species, seabirds are already experiencing shifts in migration patterns and consequently breeding grounds and patterns are changing (Visser et al. 2009; Wanless et al. 2009; Dias et al. 2011; Descamps and Strøm 2021).

Storm-petrels are a family of seabirds in the order Procellariiformes that are comprised of two families, Hydrobatidae and Oceanitidae. European Storm-petrels (*Hydrobates pelagicus*) are the smallest Atlantic seabird and are regarded as 'Least Concern' in terms of conservation efforts, due to their relatively high and stable population numbers, estimated to be approximately 459,000 to 551,000 breeding pairs (Daisy Burnell et al. 2023; BirdLife International 2024). Their distribution spans across Europe, with notable breeding populations in the Faroe Islands, United Kingdom, Iceland and Norway (Daisy Burnell et al. 2023). There are two subspecies of European Storm-petrel, the Atlantic subspecies (*Hydrobates pelagicus pelagicus*) and the Mediterranean subspecies (*Hydrobates pelagicus melitensis*) (Thomas 2024 (in-press)).

Breeding and offspring success are fundamental to ensuring the longevity of a species survival and understanding how a changing climate impacts these factors is important for future conservation measures. The significance of parental effort and climate in seabirds is well-documented, highlighting its crucial role in sustaining avian populations. Parental effort, such as nest attendance and prey delivery to Storm-petrel chicks, has been shown to directly facilitate chick growth and survival into adulthood in both *H. pelagicus* and Cape Gannets *Morus capensis* (Bolton 1995; Rishworth and Pistorius 2015).

Most studies focus on how climate can indirectly impact chick success in seabird species, where environmental changes can result in variability of parental effort. Declining levels of sea ice cover have been shown to negatively impact chick success in Wilsons Storm-petrels due to reduced food availability (Quillfeldt 2001). However, Weimerskirch et al. (2012) found that stronger wind strength indirectly benefitted breeding success of Albatrosses, by increasing travel rates and decreasing foraging distances of breeding adults, which in turn allowed increased parental effort and breeding

success. Furthermore, temperature rises have resulted in shifts in breeding seasons, with differing impacts depending upon the species. For example, lower breeding success and later breeding in Black Legged Kittiwakes *Rissa tridactyla* was associated with higher temperatures (Moe et al. 2009; Carroll et al. 2015), whereas Little Auks *Alle alle* showed earlier breeding with rising temperatures (Moe et al. 2009). Additionally, lower breeding success was shown to be linked with higher levels of rainfall in Short-tailed Shearwaters *Ardenna tenuirostris* (Price et al. 2020). Shifts in breeding seasons and foraging behaviours in seabird populations, both forms of behavioural plasticity, could help mitigate the changes in climate that are occurring.

Studies that link Storm-petrel parental care and chick success to climatic variables are limited, with most addressing how a changing climate may be impacting adult Storm-petrels and their foraging, diet, or breeding behaviour, rather than impact on the chicks. For instance, two studies found that lower temperatures during the pre-breeding period increased levels of European Storm-petrels skipping a breeding season (Soldatini et al. 2014,2016). Furthermore, European Storm-petrel nest mortality has been assessed in some studies, but generally relates to how foraging behaviour of the parent and predation impact mortality (Minguez and Oro 2003). However, very few studies directly focused on chick success and size assessed in relation to climatic conditions. Other studies have highlighted how certain nest characteristics (like dimensions and orientation) could mitigate the impact of climatic conditions on the breeding success of Wilson's Storm-petrel *Oceanites oceanicus* (Michielsen et al. 2019).

Reflecting on previous research, this study proposes to analyse how climate, through analysis of daily and inter-annual variation of climate, affects parental investment in offspring, chick growth and the overall success of offspring in *H. p. pelagicus* in Nólsoy, Faroes Islands. The Faroe Islands are a group of islands in the Northeast Atlantic Ocean, situated between Iceland and Scotland (Figure 1). The Faroe Islands are known for having one of the largest populations of breeding pairs of *H. p. pelagicus* – approximately 250,000 breeding pairs (Daisy Burnell et al. 2023) – with many colonies across the archipelago. Nólsoy is east of the Faroe Islands capital, Torshavn, and is inhabited by the largest breeding colony of European Storm-petrels globally, with approximately 50,000 breeding pairs (BirdLife International 2024). The high population makes the Nólsoy colony an ideal population to study.

Understanding how climatic variables are impacting European Storm-petrel chicks would be useful to further knowledge about Storm-petrel breeding ecology in a changing climate. This would help predict the impacts of climate change on population viability and allow conservation measures, like artificial nest boxes, to be implemented if necessary (Libois et al. 2012). This has applications in a wider

context as sea birds are crucial in connecting terrestrial and marine ecosystems by redistributing resources and are fundamental to many ecological processes. Due to this highly interconnected lifestyle, disturbances to their population numbers will consequently impact many other organisms across multiple ecosystems, which could result in huge losses to biodiversity (Signa et al. 2021).

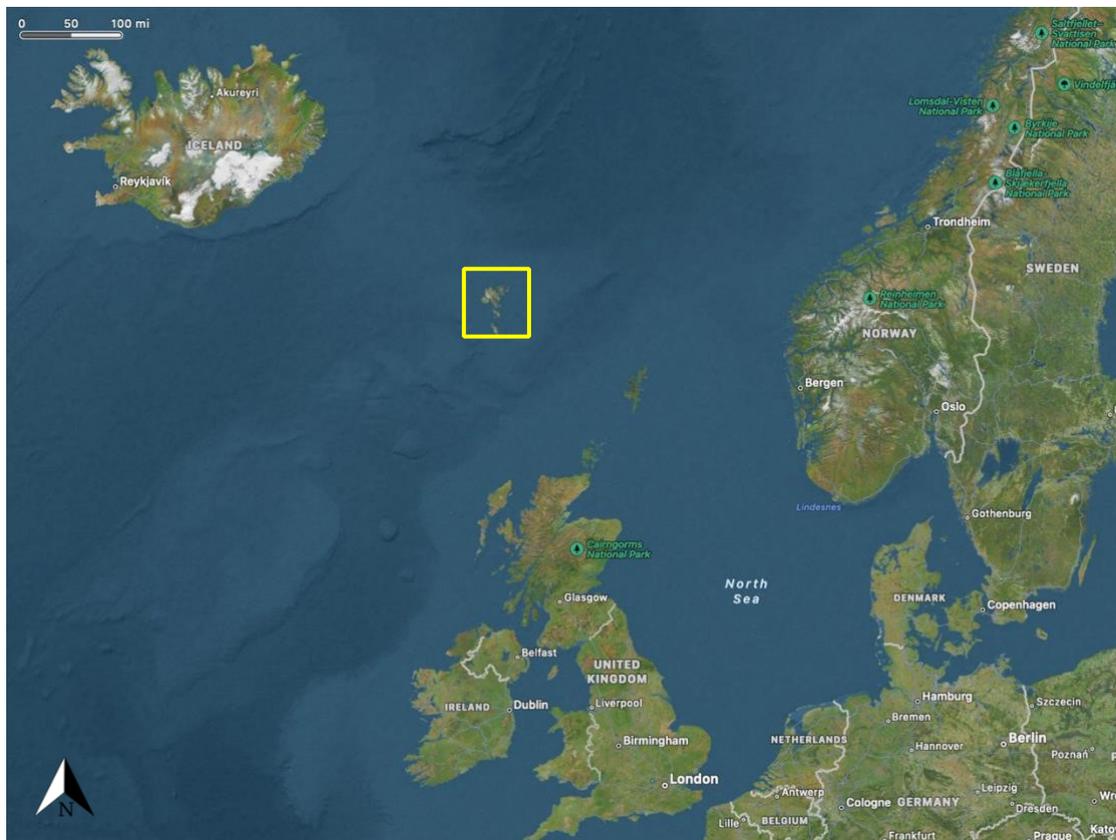


Figure 1. Map locating Faroe Islands in Europe. Yellow box shows location of the Faroe Islands.

Climate, parental provisioning, and growth of chicks are connected (e.g. Pinaud et al. 2005; Rishworth and Pistorius 2015; Christensen-Dalsgaard et al. 2018). The present study aims to understand the nature of the connection between each of these factors to determine whether climate impacts chick growth directly or alternatively affects parental effort, which in turn impacts chick growth and success. This will be done through analysis of video footage from inside artificial nestboxes on Nólsoy, Faroe Islands across two breeding periods (2022 and 2023) to assess attendance rates, incubation lengths and feeding rates, to infer parental effort, and to understand how this may vary with daily climatic changes. Additionally, I aim to assess whether hatching and fledging success are impacted by climate. Bergmann's rule states smaller individuals are found in warmer regions, since larger bodies lose heat at a lower rate, which is an adaptive advantage (Bergmann 1847). For this reason, it is predicted that chicks will be smaller in warmer breeding seasons, which would suggest lower rates of parental effort in warmer seasons

Research Questions:

1. Do daily differences in temperature, wind and precipitation levels affect the growth rate of *Hydrobates pelagicus* chicks?
2. Do daily temperature, wind and precipitation levels affect the level of parental care of *Hydrobates pelagicus*?
3. Does level of parental effort impact chick success in *Hydrobates pelagicus*?
4. Are there significant differences in overall breeding and chick fledging success in *Hydrobates pelagicus* in the Faroe Islands between the 2022 and 2023 breeding season and across each breeding season?

Methodology

Study site

This study uses data collected from a *H. p. pelagicus* colony on Nólsoy, Faroe Islands (61°59'3.839"N, 6°39'13.066"W) (Figure 2), focusing on the nesting behaviour of *H. p. pelagicus*. Data was collected by Ben Porter and colleagues from 46 and 52 artificial nest boxes that are in place across four closely situated colonies in Nólsoy over 2022 and 2023, respectively. (Table 1). In 2022, data was collated over a six-week period in between August and November, and in 2023 was collected over a threeweek period between August and September.

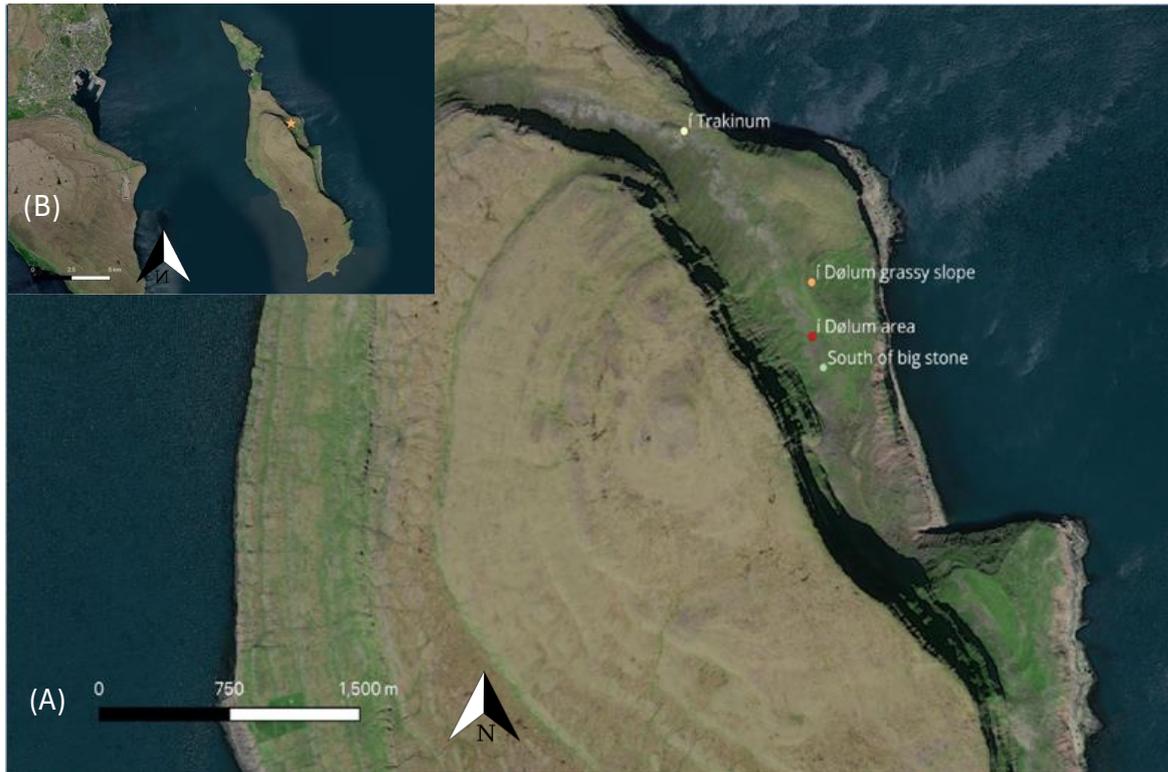


Figure 2. Map to locate the colony of the European Storm-petrels on the island of Nólsoy in the Faroe Islands, showing four main areas (A). (B) Inset locates colony in context of the whole island of Nólsoy. Maps sourced on Google earth. Information provided by Ben Porter, 2024.

Table 1. Map Coordinates for the four main areas of the *Hydrobates pelagicus* colony on Nólsoy, 2023, with nest box numbers for 2023 (Information provided by Ben Porter, 2024).

Nólsoy colony location	Coordinates of area	Nest boxes at this site
í Trakinum	61°59'43.9"N, 6°39'07.2"W	1A, 1B, 1C, 1D, 2, 3A, 3, 4, 5, 6, 7
í Dølum grassy slope	61°59'32.7"N 6°38'40.9"W	8, 9, 10, 11A, 11, 12, 13, 91, 92, 14, 15, 16A, 16B, 16C, 16, 17, 18, 19, 20, 20A, 20B
í Dølum area	61°59'27"N , 006°38'39"W	21, 22, 22A, 22B, 23, 24, 25, 26, 27, 27A, 28, 29, 30, 31, 32, 33
South of big stone	61°59'25"N , 006°38'42"W	34, 35, 36, 37

Field work

Prior to the data collection period, each nestbox was assessed to determine the status of the nest box (occupancy and if applicable, nesting stage) by *H. p. pelagicus*. Subsequently, during data collection, daily nest checks were carried out across all occupied boxes and nesting stage continued to be monitored. Once chicks had hatched, their weights were recorded daily across the collection periods (Figure 3A). Any missing days of chick weight data were due to inability to reach colony sites because of bad weather.

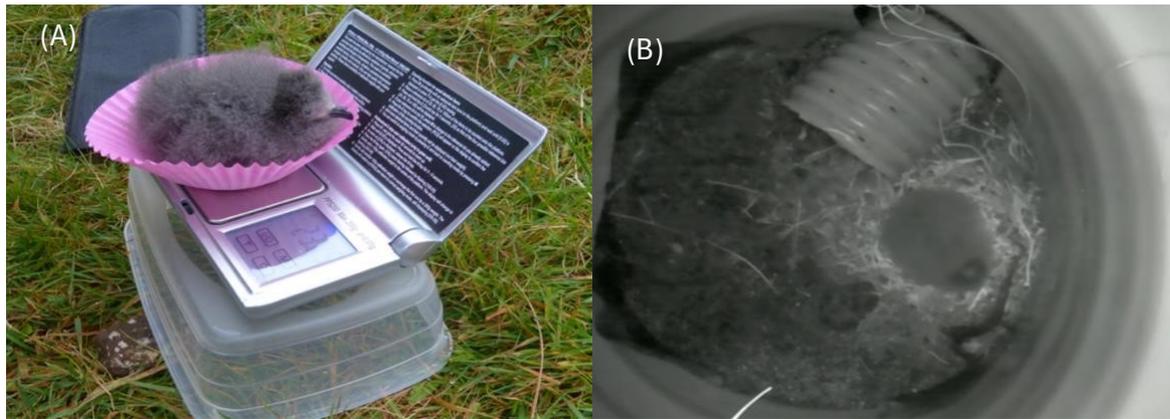


Figure 3. Photographs of data collection in Nólsoy, Faroe Island. A) Shows how chick weights would be recorded. Image taken and provided by Ben Porter ©, 2022. B) Shows a screenshot of footage collected using Raspberry Pi cameras inside artificial nest chambers.

Purpose built Raspberry Pi cameras (built following methods from Hereward et al. (2021)) were deployed strategically inside artificial nests of interest that recorded for between 8 and 25 hours at a time, with the majority being between 14 and 25 hours, dependent on power bank supply and weather causing failure, to provide insight into the breeding biology of *H. p. pelagicus* (Figure 3B). For the rest of this study, each block of 14 to 25 hours of footage will be referred to as a day of footage. Recordings would continuously run for 30 seconds at a time with an interval of 0.1 seconds between videos. In the 2022 film data, 5 nest boxes were filmed over the season for between 3 and 10 days, whilst in 2023, 9 nest boxes were filmed between 1 and 15 days.

Weather data

Weather data was sourced from R (2023. Version 12.0+369) on R-Studio using the “GSODR” Package (Sparks et al. 2017). Tórshavn (62°1'1.2"N, 6°46'1.2"W) was the nearest weather station to the nestboxes on Nólsoy, however there was insufficient weather data across both the study periods of 2022 and 2023. For this reason, weather data from Vágur (62°3'50.4"N, 7°16'37.2"W), the second nearest weather station to Nólsoy, was used for this study which was approximately 40 miles from

Nólsoy.

Statistical tests were carried out to find if the two weather stations recorded similar weather patterns. A Wilcoxon rank test showed that temperature was not significantly different between weather stations ($W = 2579$, $p = 0.5922$) and was significantly correlated ($r = 0.99$, $p < 0.0001$) (Figure 4A). Due to the lack of data in Tórshavn for wind and precipitation, comparison to Vágur weather station was invalid for these variables (Figure 4B). However, due to the similarity between temperature data in Torshavn and Vagar, and lack of any closer data, weather data from Vagar was used for this study.

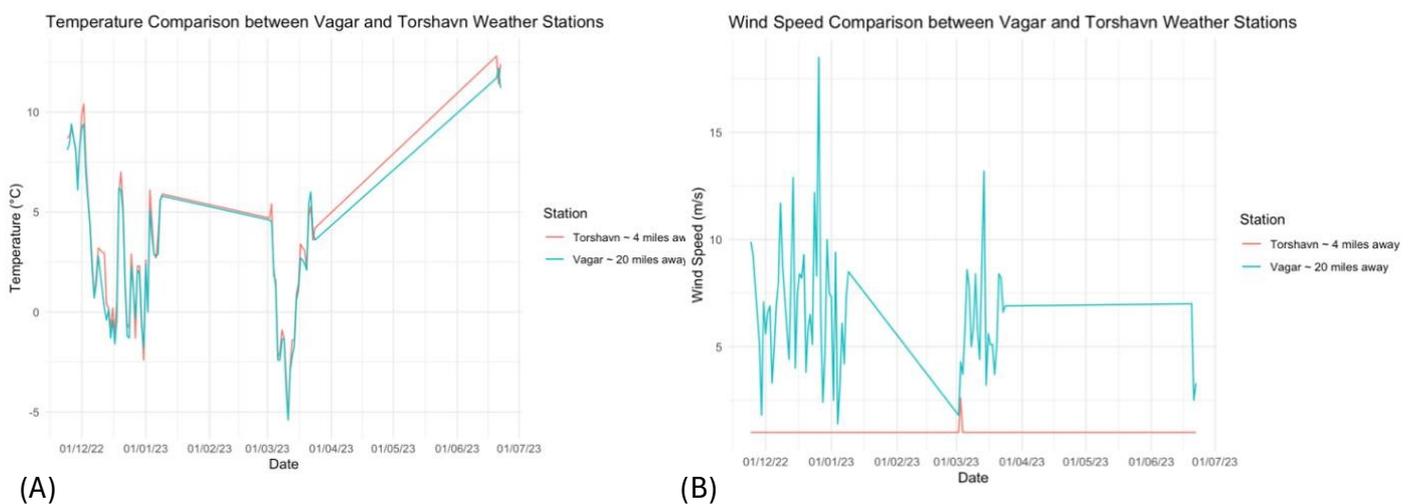


Figure 4. Weather plots across 2022 and 2023 for different climatic variables, comparing two weather stations: Vágur (blue line) and Tórshavn (red line). A) Mean temperature ($^{\circ}\text{C}$) across both weather stations. B) Mean wind speed (metres per second) across both stations

Video analysis

Video footage was utilised to determine the parental effort of *H. p. pelagicus* and interactions between the chick and parent. Due to high volume of footage captured, 1 to 2 days of footage were analysed for each nestbox, taken from both the beginning and the end of the sampling period of each nestbox, to ensure that any changes in behaviours were recorded. In this study, box-to-box comparison between years was not possible because the on-site artificial nestbox numbers were changed in between 2022 and 2023.

Video footage was watched using Elmedia Video Player (2023 Version 8.17(3393)) and time stamps on every 30 second video allowed behaviours to be recorded according to time of day and duration (to a degree of accuracy of 10 seconds). If parent(s) were not present in the video clip, footage would be played at high speed until parent entered the nest box, when it would be slowed to real-time, and behaviours would be recorded. A variety of behaviours were being observed, such as feeding events,

incubation of a chick or an egg by the parent, and duration parents left chicks unattended (Table 2). Behaviours were recorded in two ways: real-time start and end of observations and durations of observations, which were then standardised across nest boxes into a proportion of time, to account for differences in footage length.

Table 2. Nesting behaviours analysed during video analysis and information gained from each observation.

Observations recorded	Definition	Ascertained
Feeding	Chick observed with bill inside parent's bill	Feeding duration (Number of minutes that a single feeding event lasted) Duration between feeds Feeding rates per hour (number of feeding events divided by the hours of footage recorded).
Incubation of egg	Parent on top of egg	Duration of incubation of egg
Incubating chick	Parent on top of chick	Duration of incubation of chick Proportion of incubation time that was in the day or the night*
Chick unattended	Parent leaving nestbox, leaving chick alone inside nest box	Duration of time unattended Time of day unattended

**To decipher day and night time incubations, periods of time were determined using average sunset and sunrise times for September in Nólsoy, Faroe Islands, which can be found here: <https://www.weather-atlas.com/en/faroe-islands/nolsoy-weather-september>. Sunrise (6:15AM), sunset (8:37PM).*

Data analysis

Additional data collected during fieldwork in Nólsoy for both 2022 and 2023 was provided by Ben Porter, containing information on hatch dates, fledging dates, chick weights across the season, and overall success in each monitored box. All data was manipulated and analysed in R (2023. Version 12.0+369) on R-Studio. The package “lubridate” was used to format dates and time durations in the data used in this study (Grolemund and Wickham 2011).

Bar charts were created using the “ggplot2” (Wickham 2016) R Studio package to show overall success in the monitored artificial nest boxes across 2022 and 2023. Chi-squared and Fishers Exact

tests were carried out to assess annual differences in breeding parameters ($p < 0.05$). Statistical tests were used to show if weather significantly differed between 2022 and 2023, according to mean temperature ($^{\circ}\text{C}$), mean wind speed (m/s) and rain occurrence.

A summary of all general linear models (GLMs) used for this study, showing all variables, are summarised in Appendix 1. A GLM (family = Gaussian, link = "identity") was used to test whether chick weight differed, controlled by age of chick (days), between years or according to Julian day. Throughout this study, the variable Julian day refers to the hatch date of chick, formatted as the number of days from January 1st of that year.

To determine how chick growth and climate interact, a GLM (family = Gaussian, link = "identity") was used to test whether climatic variables impacted chick weights. The same climatic variables were used in all GLMs for this study, which were mean temperature ($^{\circ}\text{C}$), mean wind speed (m/s), and rain occurrence (where 1 = rain occurred and 0 = no rain occurred that day). Other independent variables accounted for in this GLM included age of chick (days), Julian day and year, to factor in daily and yearly difference and chick weight at different ages.

Multiple GLMs were done to find whether parental effort is impacted by climate levels (Appendix 1) using the R-Studio "betareg" package (Cribari-Neto and Zeileis 2010). To assess how the proportion of time a chick was unattended by parent was impacted by climatic variables a GLM (family = betareg, link = "logit", link.phi = "identity") was used. The same type of GLM was redone, but with proportion of time a chick was incubated by parents as the dependent variable instead of proportion of time unattended. Three more GLMs (all family = Gaussian, link = "identity") - to find whether feeding rate, feed duration and feed intervals were affected by climate - were used to test for significant effects of each independent variable, and the drop 1 function Chi tests were carried out for each GLM (significance threshold: $p < 0.05$).

All previously discussed GLMs were plotted using base R packages, with lines of best fit accounting for all variables, where the variables that were not being visualised set at their mean values.

A final GLM (family = Gaussian, link = "identity") was used to find associations between chick weight with parental effort variables (Appendix 1), to determine if parental care has a significant impact on chick weight. Drop 1 Chi tests were done to test for significant effects of each independent variable ($p < 0.05$). To account for individual differences in parental care, the box number was included as an

independent variable in this GLM. The results of these tests were visualised using the R-Studio “car” package (Fox and Weisberg 2019) as partial residual plots.

Results

Summary of trends

In 2022 46 nest boxes were monitored for breeding activity across the data collection period, whilst in 2023, 58 nest boxes were monitored. Breeding activity and success was recorded over the season (Figure 5). For all variables measured, 2023 had higher percentages, nevertheless, no significant differences were found for these breeding parameters between 2022 and 2023 except in the percentage of chicks fledged, which were significantly lower in 2022 (Table 3).

Generally, a similar pattern is observed between each breeding parameter across the two years, while different in scale, from percentage of nests made to chicks and eggs failed (Figure 5). However, the only difference to this pattern is the difference between percentage of chicks failing compared to egg stages failing. In 2022, 2.17 % eggs failed, and 13.00 % chicks failed, whilst in 2023 the percentage of chick and egg failure was the same, at 8.62 % (Table 3). A greater percentage of chicks failed in 2022 than 2023, however the difference was not statistically significant.

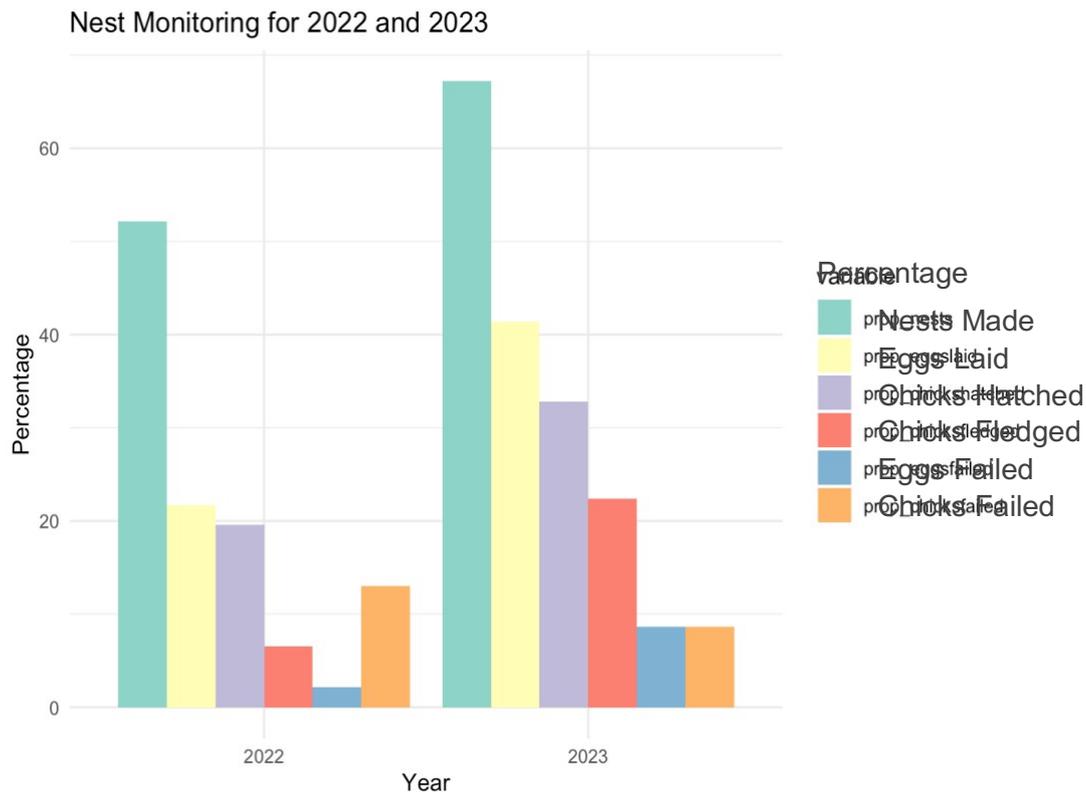


Figure 5. Overall nest data for *H. p. pelagicus* in Nólsoy, Faroe Islands in 2022 and 2023. Data is described as a percentage of all nests monitored in each breeding season. Raw data provided by Ben Porter.

Table 3. Breeding parameters observed in each year (2022 and 2023). Values are a percentage of all boxes monitored that year. Chi-squared tests carried out for yearly differences in: nests made, eggs laid, chicks hatched, and chicks fledged. Fisher’s exact tests used to analyse yearly differences in eggs failed and chicks failed. χ^2 = chi-squared value. Df = degrees of freedom.

	2022	2023	χ^2	p-value	df
Nests made	52.17 %	67.24 %	1.849	0.174	1
Eggs Laid	21.74 %	41.38 %	3.649	0.056	1
Chicks Hatched	19.57 %	32.76 %	1.649	0.199	1
Chicks Fledged	6.52 %	22.40 %	3.831	0.050	1
			Fishers exact test		
Eggs Failed	2.17 %	8.62 %	NA	0.224	1
Chicks Failed	13.00 %	8.62 %	NA	0.5313	1

Inter-annual and daily differences

There is a significant association between age of chick, Julian day and chick weight (Figure 6A), suggesting that the time of year a chick was born can affect their growth. Julian day refers to date hatched. GLM analysis (family = Gaussian, link = "identity") revealed a highly significant relationship between Julian day and chick weight, suggesting that *H. pelagicus* chicks hatched later in the year are lighter (mean decrease of 0.213 ± 0.057 grams per day, $t = -3.735$, $p = 0.000279$) (Appendix 1). Chick weight and their ages are significantly associated, with every day older they become they are expected to increase in weight (0.885 ± 0.060 g per day, $t = 14.733$, $p < 0.0001$) (Appendix 1). Body mass is shown to increase rapidly within the first 30 days of life up to approximately 30 to 40 grams, then a plateau is observed (Figure 6). Annual differences in chick weight were not significant between 2022 and 2023 (increase from 2022 to 2023 of 1.324 ± 1.008 grams, $t = 1.313$, $p = 0.192$) (Figure 6B).

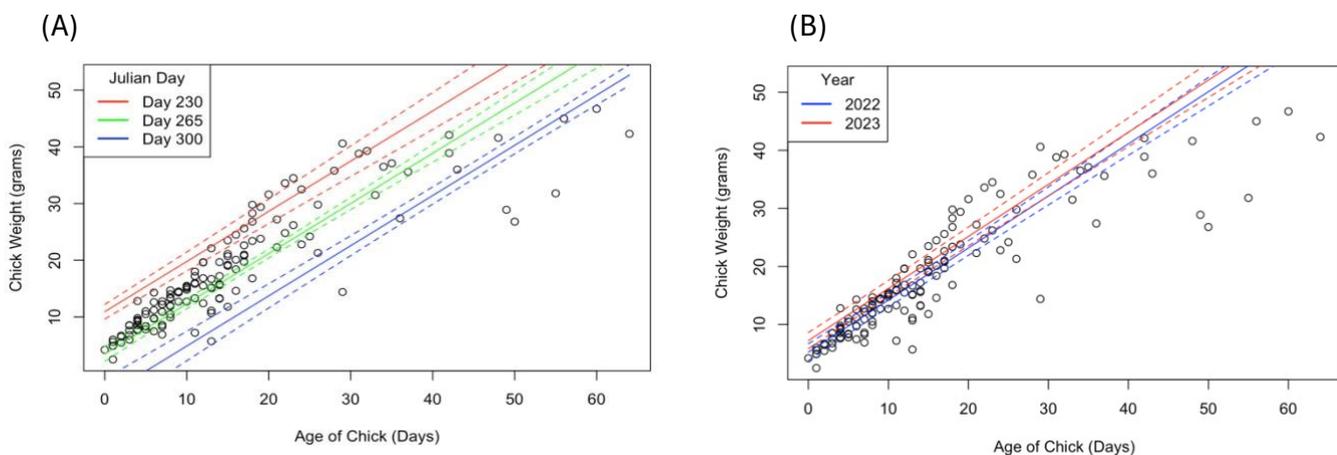


Figure 6. Association between Age of Chick (days) and Chick Weight (g), and how the Julian Day of chick's hatching date (A) and breeding year (B) affects the relationship. Controlled to set in year 2023. Fit lines show how predicted chick weight varies with age, with other variables in models held constant at their mean value (unless otherwise shown). Dashed lines show standard error around each line of fit.

Climate and chick growth

To explore the significant association between chick growth and Julian day, chick growth and parental provisioning rates were analysed with respect to their response to different climatic variables and each other, to establish the determining factors.

A GLM (family = Gaussian, link = "identity") was executed to assess how climate affects chick weights (Appendix 1). Chick weight was non-significantly associated with mean wind speed (m/s) (and rain

occurrence is found to have little effect on the weights of chicks across both years of data). As highlighted in the previous analysis, age of the chick and Julian day were still significantly associated with weight of the chick in this GLM, where climatic variables were the other independent variables. The mean temperature was found to be a significant determining factor of chick weight, with a positive correlation between the two variables observed ($t = 2.732$, $p=0.00718$) (Figure 7). The effect of temperature across different age chicks is very similar (Figure 7A), where chick weight is observed to be higher with warmer mean temperatures. The GLM showed that for every 1 °C rise in temperature, chick weight is expected to increase by 0.613 ± 0.224 g per day (Appendix 1).

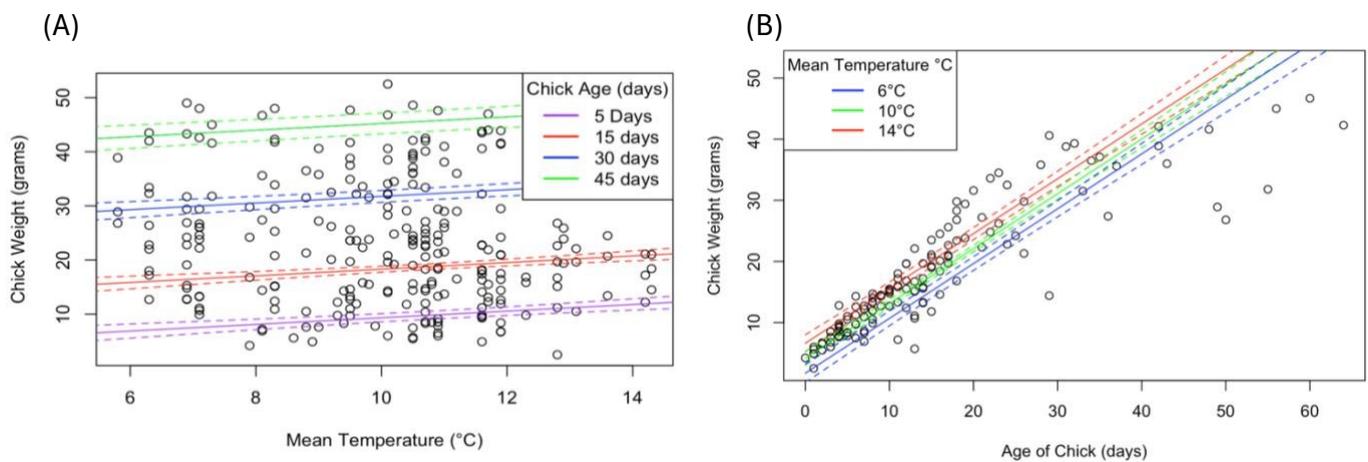


Figure 7. Relationship between chick weights of *H. pelagicus* and mean temperature (°C) shown according to chick age. A) Shows how relationship between chick weight (grams) and mean temperature (°C) is affected by age of chick. Fit lines for different aged chicks (see key). B) Shows chick growth, plotting age (days) against weight of chick. Lines show how different temperature affects chick weight according to age. Fit lines for different temperatures (see key). Dashed lines indicate standard error of each fit line.

Climate and parental care

GLM analysis (family = betareg, link = “logit”, link.phi = “identity”) found that the proportion of time that a chick was left unattended, the proportion of time parents spent brooding their chick, and interval between feeding events were not significantly associated with mean wind speed, mean temperature, or rain presence (see Appendix 1). However, an effect of the presence of rain was found on both the feeding rate per hour and duration of feeds with the presence of rain (Figure 8A and B). Chi tests (using the drop 1 function) on GLM analyses (both family = Gaussian, link = “identity”) showed significant associations between feeding rate and presence of rain (chi-squared = 0.0729, degrees of freedom = 1, $p = 0.01425$) and between feeding duration and rain presence (chi-squared = 163.18, degrees of freedom = 1, $p= 0.04482$). In the presence of rain, feed duration was generally higher

(increasing by 1.62 ± 0.86 minutes – Appendix 1) (Figure 8A). The range of feed durations was shorter in the presence of rain (approximately within a 5-minute range) compared to the absence of rain (approximately an 8 minute range). Opposingly, feeding rate was found to decline with the presence of rain (decreasing by 0.107 ± 0.05 feeds per hour – Appendix 1) (figure 8B).

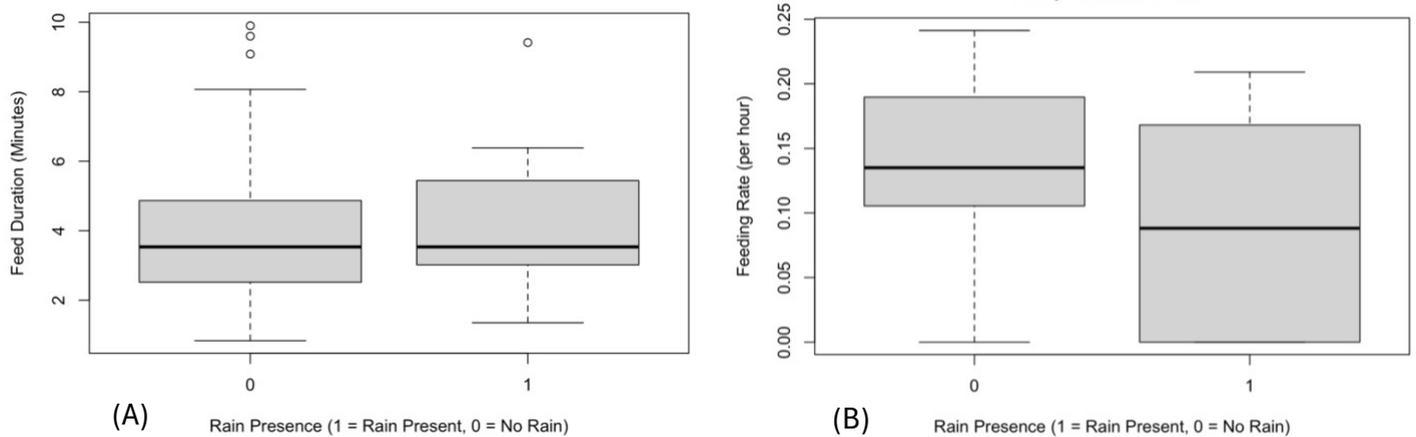


Figure 8. Relationships between A) Feed duration and B) Feeding rate, with rain occurrence. 1 = Rain Occurred, 0 = No Rain Present)

Parental care and chick growth

GLM analysis (family = Gaussian, link = “identity”) on how chick weight is affected by parental care, found that proportion of time spent brooding a chick and proportion of time the chick is unattended to be important determining factors of chick weight, where increases in proportions were associated with decreases in chick weight (Figure 9A and B). Chick weight was shown to significantly decrease under increasing proportion of time spent incubated (mean decrease of 17.906 ± 5.372 grams, $t = -3.333$, $p = 0.0028$) and time unattended (mean decrease of 22.487 ± 5.494 grams, $t = -4.093$, $p = 0.0004$). However, chick weight was not significantly associated with feed duration (-0.187 ± 0.133 grams, $t = -1.406$, $p = 0.172$), feeding rate (-11.708 ± 7.612 grams, $t = -1.538$, $p = 0.137$) or feed intervals (0.059 ± 0.111 grams, $t = 0.531$, $p = 0.600$). Feeding rate, feeding intervals and feed durations demonstrated non-linear relationships with chick weight (Figure 9C-E). Chick weight is not affected by feeding rate until it increases over 0.15 feeds per hour, where a decrease in chick weight is observed over this threshold of feeds (Figure 9C).

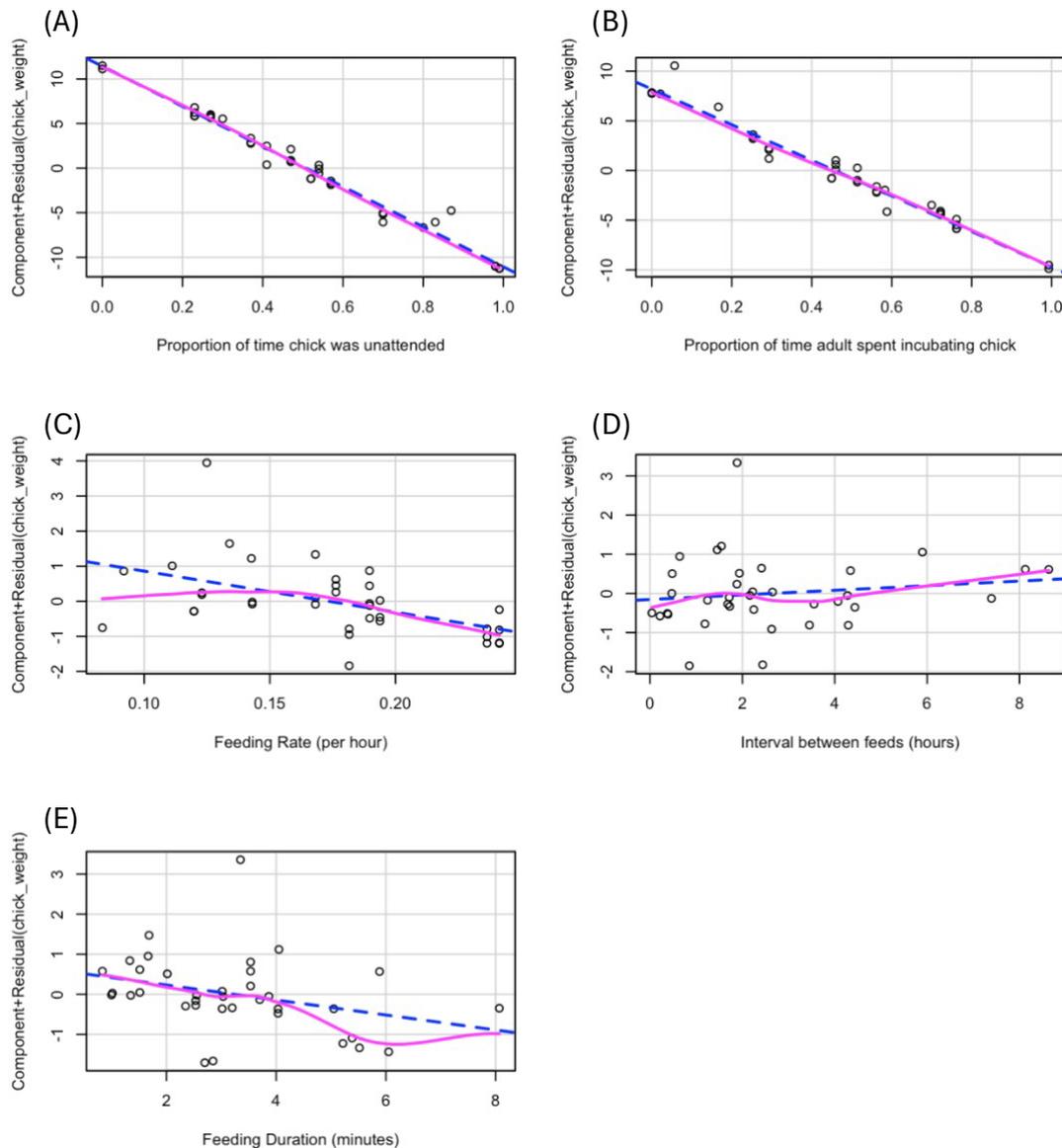


Figure 9. Partial residual plots showing how parental effort impacts chick weight, controlling for all the other factors using their mean value (Julian day hatched, age of chick, box number). Y-axis refers to the relative weight of the chick (grams). Blue dashed lines show where the linear relationship would follow, and pink line show the actual relationship between relative chick weight and provisioning variable. A) Shows relationship between the proportion of time a chick was unattended and its effect on chick weight. B) Shows relationship between the proportion of time a chick was brooded by the parents once hatched and its effect on chick weight. C) Shows relationship between the feeding rate of the parent (feeds per hour) and its effect on chick weight. D) Shows relationship between the number of hours between feeding events (hours) and its effect on chick weight. E) Shows relationship between the duration of a single feed (minutes) and its effect on chick weight.

Discussion

The aim of this study was to analyse whether climate had an impact on chick growth and success and determine whether this impact was a direct effect of climate, or an indirect effect via the impact climate may have on parental effort. Associations between the following were investigated: climate and chick growth; climate and parental care; and parental care and chick growth of *H. p. pelagicus*. We aimed to determine if there were any differences in overall breeding success between 2022 and 2023 at Nólsoy and found that significantly more chicks fledged in 2023 than 2022. Significant associations were discovered between temperature and chick growth, but no relationship was determined with wind or rain presence. Interestingly, the only relationship discovered with climatic variables and parental care was between feed duration or feeding rate with rain presence. Strong linear relationships were found between chick weight with proportion of time a chick was incubated and unattended.

Overall success

No overall differences were found between 2022 and 2023 for the percentages of eggs laid, chicks hatched, eggs failed, and chicks failed at the monitored nest boxes in Nólsoy. However, significantly fewer chicks fledged in 2022 than 2023. This suggests a better reproductive success in 2023 than in 2022 in Nólsoy, although a multitude of factors could have contributed to these results. It was brought to our attention that a storm occurred on Nólsoy in September 2022 (hypothesised to be where peak wind is observed – Appendix 2E), which due to the categorical nature of weather data for rain, was not evident in the analyses of this study. Extreme climatic events, like storms, have been shown to negatively impact the overall breeding success in *H. p. pelagicus* and other seabirds (Newell et al. 2015; Zuberogitia et al. 2016), and negatively affect the fledging success specifically in Manx Shearwaters *Puffinus puffinus* (Baker 2019).

The North Atlantic Oscillation (NAO) Index supports the results of overall success in this study. The NAO Index informs on the differences in atmospheric pressure over the northern Atlantic Ocean, where negative values suggest drier and cooler climate over North Europe and positive values indicate wetter, stormier and milder conditions in North Europe (Draycott 2012). Interestingly, between August and November 2023, the NAO index remained negative throughout, where overall breeding success was better, and between August and November 2022 the NAO Index fluctuated between positive and negative values (NOAA 2024) (see Appendix 4 for NAO Index values). This highlights the possibility that the weather conditions associated with the NAO could be influencing the overall success of *H. p. pelagicus* chicks, and in future it is recommended to explore this possible association in more depth, with statistical analyses.

In long-lived birds, including *H. pelagicus*, the success of breeding can be influenced by the age of the breeding parents, which was not measured in this study. Nonetheless, within the literature opposing findings exist, debating whether older or younger birds exhibit superior breeding success. For example, Hernández et al. (2017) found that younger breeding parents had significantly better success, whilst contrastingly Limmer and Becker (2010) found that with age and breeding experience, success improved in long lived seabirds. While parental age was not considered in this study, its inclusion in future studies could potentially aid explanation of certain inter-annual differences in breeding success, albeit mechanisms remain unresolved.

Furthermore, extreme events in the pre-breeding season that impact the surrounding environment could have contributed to differences in the overall breeding success found in this study between 2022 and 2023. *H. pelagicus* has been shown to exhibit behavioural plasticity in regard to environmental conditions which are unfavourable for their own survival, and when extreme events occur, such as a period of storms or oil spills, or unfavourable climate, they have been observed to skip the breeding season altogether (Zabala et al. 2011; Soldatini et al. 2014,2016; Zuberogoitia et al. 2016). The negative impact on breeding success may be exacerbated by inexperienced, younger storm-petrels attempting to breed in unfavourable conditions (Newell et al. 2015; Zuberogoitia et al. 2016). In future studies on Nólsoy regarding climate's effect on reproduction of *H. pelagicus*, it would be beneficial to study the pre-breeding season weather to assess any extreme climatic events alongside ages of breeding birds, to account for any skewed results that may occur.

Climate and chick growth

This study found a significant positive association between chick weight and temperature. Unexpectedly, these results diverge from Bergmann's rule, which posits that larger individuals of a species are found in colder areas due to their ability to retain more heat (Bergmann 1847). However, the relevance of applying Bergmann's rule to temperature variations at this scale remains uncertain, as in the literature it has been primarily applied to latitudinal temperature gradients (e.g. Jakubas et al. 2014; Yamamoto et al. 2016; Piña-Ortiz et al. 2023). Interestingly, previous literature finds successful application of Bergmann's rule in *H. pelagicus* adults at the same colony as studied in this report, demonstrating increasing wing span with latitude, suggesting a correlation with temperature (Jakubas et al. 2014).

Furthermore, it is unclear whether Bergmann's rule is applicable to Storm-petrels during their early development and growth, because energy demands may differ considerably to fully grown adults. Storm-petrels can be altricial, meaning they rely on parents for warmth and food, which could suggest

that in their early development they would not be as strongly affected by environmental temperatures since they are constantly being brooded by parents to maintain their body temperature (Visser 2001; Thomas 2024 (in-press)).

Contrary to much of the previous literature, association was absent between wind or rain occurrence with chick growth across the breeding seasons in Nólsoy. An important aspect to consider is that the precipitation data used in this study lacked quantification of rainfall intensity or duration at Vágur, which may have provided useful insights into any correlation between chick growth and strength of rainfall. Price et al. (2020) found that increased levels of rainfall occurred in breeding seasons of shorttailed shearwaters *Ardenna tenuirostris* with lower reproductive success, which highlights the significance rainfall measurements could have had in this study. It is difficult to be conclusive on the nature of the relationship between rainfall and chick growth in this study in the context of the European Storm-petrel, as it is difficult to detect a relationship by solely using a categorical variable for rain occurrence. It is recommended that, in future, full precipitation measurements are used to assess this association.

While our study found no correlation between daily mean wind speed and chick growth, other research found significant relationships between these variables. Most studies found a negative impact of wind strength on survival and growth (Jakubas et al. 2014; Christensen-Dalsgaard et al. 2018), although may not directly relate to hindering growth but relate to reduced chick survival through strong wind destroying nests. Since *H. pelagicus* chicks were hatched inside artificial nest boxes in this study, it could mean that chicks were more sheltered from natural elements, like wind or precipitation, than in other studies (for example, Christensen-Dalsgaard et al. 2018 studied effect of wind on natural nests), thus were less impacted by climate. The findings of this study highlight the potential conservation value of artificial nest boxes in a changing climate, as most studies find wind or precipitation to have a negative impact on fledging success of *H. pelagicus* chicks.

The discrepancies between this study to other findings may be a result of the internal microclimate of artificial nest boxes, which could disguise previously identified relationships between climate and chick growth and success. Thermal microclimates within natural nests can be notably different to external climate, with evidence to suggest that this difference is exacerbated in artificial nest boxes due to their human design with better insulated materials, put in place as conservation measures (Hart et al. 2016; Michielsen et al. 2019). Nest orientation, insulation and entrance size are among some of the factors which impact thermal and wind exposure to the nest and consequently the chick (Michielsen et al. 2019), which could have played a role in overall breeding success in this study.

Climate, parental care and chick growth

Whilst we found significant associations between growth and temperature, no such relationship was established between chick growth and wind or precipitation directly. Due to previous literature finding relationship between these variables, it was possible that wind, precipitation and temperature impacts parental care which in turn affects chick growth. Significant associations between rain occurrence with feeding rate and feed duration were found in this study, where generally feeding rate declined with rain, and feed duration increased with rain occurrence. Although no association between climate and proportion of time a chick is unattended were found, the fact that feeding rates decline with rain occurrence could suggest that parents spend more time foraging, possibly due to lower prey availability associated with rainfall. Interestingly, in this study feeding rate and duration showed a nonsignificant but negative correlation with chick weight. Finney et al. (1999) found that in unfavourable weather conditions, such as precipitation, the Common Guillemot *Uria aalge* altered their foraging sites which resulted in changes in prey composition that were less nutrient rich, and consequently negatively impacted chick weight. This could be a possible explanation for the effect of feeding rate and duration on chick weight found in this study. It is unclear why feed duration increased with rain occurrence, but it could be a behavioural adaptation to compensate for less frequent feeding.

A possible explanation for the reason feeding rate declined with rain presence, while attendance and incubation rates were not significantly affected by any climatic variables, could be related to the fixed investment hypothesis (Navarro and González-Solís 2007). This is a hypothesis where parents make a trade-off between investment into current chick and into themselves (to ensure continued reproduction) under environmental stress like precipitation, where they adapt their provisioning dependent on their own requirements. This could explain that under poor weather conditions, parents may be present at the nest but may not feed very often to preserve food and energy expenditure for their own benefit.

This study found a significant negative association between the time that chicks were unattended with chick weight. Rishworth and Pistorius (2015) supports this finding, where they found that the more time a parent spent away foraging, suggesting offspring was left unattended, provisioning rates to their chicks decreased which slowed daily growth. The proportion of time chicks were incubated was also found to be significantly associated with chick weight declining. This result is unexpected due to the breeding biology of birds, where it is known that chicks require heat from parents to grow, especially in their brooding period or until development of homeothermy (Visser 2001). Whilst this result is unexpected, it could highlight that potentially other factors have a greater impact on chick weight.

Conclusions and future directions

Climate was a determining factor of chick growth in *H. p. pelagicus* in Nólsoy over 2022 and 2023. It is hard to explicitly establish whether chick growth is directly impacted by climate due to the effects it could have on energy expenditure, or whether it impacts the parental provisioning provided to chicks. Temperature was found to play a significant role in benefitting chick growth directly, most likely due to energy requirements of young chicks. Wind and precipitation did not directly affect chick growth, but precipitation did affect parental provisioning, through declined feeding rate and increase feeding durations. It may not be as straightforward as a direct or an indirect effect of climate on chick growth, but a multifaceted, complex relationship between these variables simultaneously.

Overall reproductive success was better in 2023 than in 2022 in Nólsoy, with notably better fledging success in 2023. This may be attributable to a negative NAO Index throughout the 2023 breeding season, contributing to calmer, drier weather conditions. However, it would be recommended that further statistical analyses are done in future to investigate this.

Potentially, other unidentified confounding variables, such as parental age and weather conditions during the pre-breeding season, could affect the way in which climate impacts chick weight across the season, in addition to the overall breeding success. Inclusion of these in future studies would help clarify relationships between climate, parental provisioning, and chick growth of *H. p. pelagicus*. To improve this study, it would be beneficial to obtain precipitation data of greater resolution to determine the exact effects of rainfall on chick growth and parental provisioning in *H. p. pelagicus*.

Furthermore, this study highlights the conservation value of artificial nest boxes as a buffer against weather conditions, which are expected to worsen with climate change, since most of the relationships between weather and chick growth in this study either opposed the literature (such as temperature effects) or were non-existent (such as wind or precipitation).

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Appendix

Appendix 1. Detailed breakdown of all General Linear Models (GLMs) and the variables used in each test. Results shown for GLM and chi tests (using the drop1 function on RStudio). If family = betareg, no chi test was done. If family = gaussian, chi test was done. In GLM results, tvalues provided if family = Gaussian, z values provided if family = betareg.

Type of GLM	Dependent Variable	Independent Variable(s)	GLM Results				Chi test results (using drop 1)				
			Est.	SE	t (or z) value	p-value	D f	Dev	AIC	ScaledDev	p-value
Family = Gaussian, link = "identity"	Chick weight (grams)	Age of chick (days)	0.88532	0.06009	14.733	<0.0001 (***)	1	7469.9	932.92	131.924	<0.00005 (***)
		Julian day hatched	-0.21305	0.05704	-3.735	0.000279 (***)	1	3110.8	814.66	13.663	0.0002187 (***)
		Year	1.32357	1.00819	1.313	0.191541	1	2848.4	802.76	1.765	0.1840613
Family = Gaussian, link = "identity"	Chick weight (grams)	Age of chick (days)	0.89721	0.05910	15.180	<0.0001 (***)	1	7218.3	934.29	139.016	<0.00005 (***)
		Julian day hatched	-0.17199	0.05842	-2.944	0.00385 (**)	1	2752.2	804.12	8.845	0.002939 (**)
		Year	1.99460	1.01768	1.960	0.05218	1	2655.0	799.27	3.992	0.045722 (*)
		Mean temperature (°C)	0.61338	0.22449	2.732	0.00718 (**)	1	2728.0	802.93	7.653	0.005669 (**)
		Mean wind speed (m/s)	-0.29207	0.21355	-1.368	0.17381	1	2615.3	797.23	1.959	0.161668
		Rain occurrence	1.22211	1.28828	0.949	0.34459	1	2595.7	796.22	0.946	0.330790
family = betareg, link = "logit",	Proportion of time chick was unattended	Age of chick (days)	0.22438	0.08010	2.801	0.00509 (**)	NA				
		Julian day hatched	0.02714	0.08512	0.319	0.74982					
		Year	-0.82240	1.02624	-0.801	0.44292					

link.phi = "identity"	Mean temperature (°C)	-0.33330	0.20196	-1.650	0.09887
	Mean wind speed (m/s)	-0.15847	0.28387	-0.558	0.57667
	Rain occurrence	-0.13860	0.79910	-0.173	0.86231

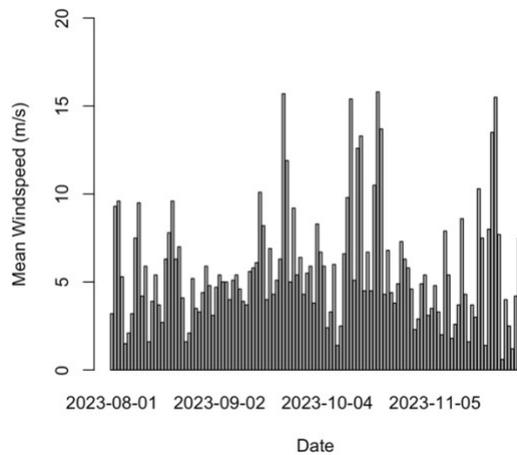
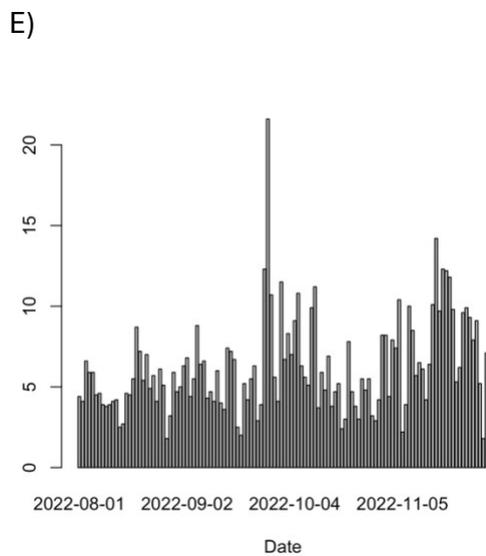
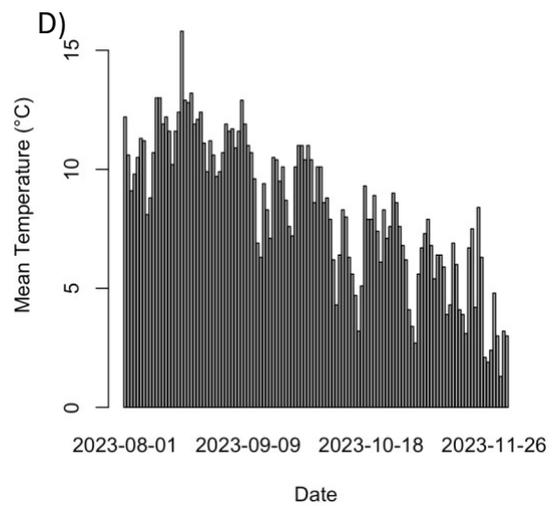
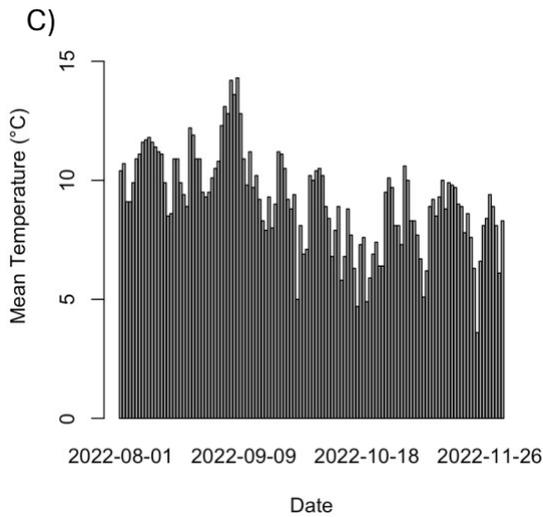
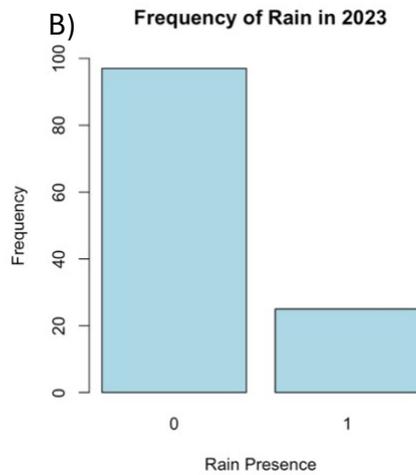
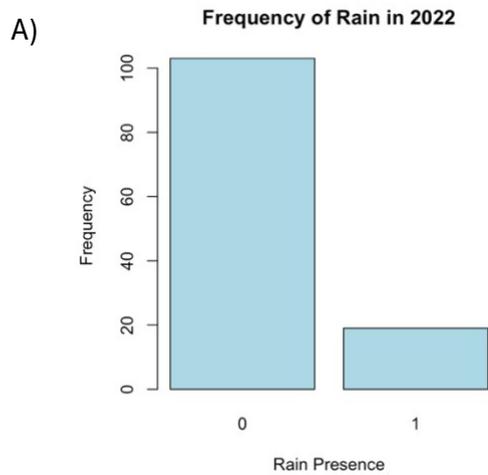
family = betareg, link = "logit", link.phi = "identity"	Proportion of time chick was incubated	Age of chick (days)	-0.16484	0.07501	-2.198	0.0280 (*)	NA				
		Julian day hatched	-0.14555	0.08299	-1.754	0.0795					
		Year	2.35603	1.01493	2.321	0.0203 (*)					
		Mean temperature (°C)	0.29833	0.19004	1.570	0.1165					
		Mean wind speed (m/s)	0.29937	0.26786	1.118	0.2637					
		Rain occurrence	-0.42543	0.76078	-0.559	0.5760					
Family = Gaussian, link = "identity"	Feeding rate (feeds per hour)	Age of chick (days)	-0.00089	0.00485	-0.183	0.8578	1	0.05487	-51.297	0.0499	0.82322
		Julian day hatched	-0.00037	0.00552	-0.667	0.5158	1	0.05648	-50.691	0.6563	0.41785
		Year	0.07393	0.06508	1.136	0.2751	1	0.05979	-49.496	1.8512	0.17364
		Mean temperature (°C)	0.01030	0.01285	0.801	0.4365	1	0.05725	-50.406	0.9412	0.33198
		Mean wind speed (m/s)	0.00974	0.01791	0.544	0.5951	1	0.05590	-50.908	0.4391	0.50755
		Rain occurrence	-0.10695	0.04967	-2.153	0.0492 (*)	1	0.07287	-45.340	6.0066	0.01425
Family = Gaussian,		Age of chick (days)	-0.06085	0.16666	-0.365	0.717	1	151.69	222.14	0.1568	0.69214

link = "identity"	Feed duration (minutes)	Julian day hatched	-0.04189	0.09002	-0.465	0.644	1	151.97	222.24	0.2545	0.61395
		Year	-0.92452	1.19451	-0.774	0.443	1	153.26	222.68	0.7009	0.40249
		Mean temperature (°C)	0.03113	0.29038	0.107	0.915	1	151.28	222.00	0.0135	0.90737
		Mean wind speed (m/s)	0.25308	0.22564	1.122	0.268	1	155.47	223.44	1.4613	0.22672
		Rain occurrence	1.62299	0.86129	1.884	0.066	1	163.18	226.01	4.0253	0.04482 (*)
		Chick weight	0.15087	0.12998	1.161	0.252	1	155.77	223.55	1.5636	0.21115
Family = Gaussian,	Interval between	Age of chick (days)	-0.4100	1.0512	-0.390	0.699	1	8185.5	354.63	0.18219	0.6695

link = "identity"	feeding events (hours)	Julian day hatched	0.2916	0.8466	0.344	0.733	1	8177.7	354.59	0.14208	0.7062
		Year	0.4682	11.3832	0.041	0.967	1	8150.4	354.45	0.00203	0.9641
		Mean temperature (°C)	-0.3048	2.6622	-0.114	0.910	1	8153.1	354.47	0.01572	0.9002
		Rain occurrence	-2.6248	6.9960	-0.375	0.710	1	8182.8	354.62	0.16858	0.6814
		Mean wind speed (m/s)	2.6752	2.0725	0.205	0.205	1	8538.0	356.4	1.95330	0.1622
Family = Gaussian, link = "identity"	Chick weight (grams)	Age of chick (days)	-0.12666	0.58750	-0.216	0.831128	1	28.675	117.97	0.070	0.7918439
		Julian day hatched	1.10645	0.56174	1.970	0.060522	1	33.246	123.3	5.394	0.0202023 (*)
		Box 5	- 16.17764	6.14279	-2.634	0.014553 (*)	4	179.832	178.07	66.166	<0.00005 (***)
		Box 10	3.28153	0.84801	3.870	0.000732 (***)					
		Box 22	- 17.10624	9.50747	-1.799	0.084568					

Box 31	-9.40818	4.19041	-2.245	0.034239 (*)					
Feed duration	-0.18717	0.13311	-1.406	0.172488	1	30.977	120.75	2.850	0.0913664
Feed interval	0.05877	0.11067	0.531	0.600288	1	28.956	118.33	0.421	0.5166874
Feeding rate	11.70787	7.61238	-1.538	0.137129	1	31.440	121.29	3.384	0.0658309
Proportion incubation	- 17.90613	5.37239	-3.333	0.002779 (**)	1	41.866	131.6	13.694	0.0002151 (***)
Proportion unattended	- 22.48742	5.49404	-4.093	0.000416 (***)	1	48.597	136.97	19.061	<0.00005 (***)

Appendix 2. Summary of weather data across 2022 and 2023 in Vágur, Faroe Islands. A) Shows Rain occurrence in 2022, where 0 = number of days with no rain, and 1 = number of days where rain occurred. B) Shows Rain occurrence in 2023, where 0 = number of days with no rain, and 1 = number of days where rain occurred. C) Mean temperatures (°C) between August and November 2022. D) Mean temperatures (°C) between August and November 2023. E) Mean wind speeds (m/s) between August and November 2022. F) Mean wind speeds (m/s) between August and November 2023.



Appendix 3. Statistical tests showing whether significant differences exist between value of weather variable between August to November 2022 and 2023. **A)** Welch's t-test for mean temperatures (°C) and mean wind speed (m/s) at Vagar, Faroe Islands. **B)** Fisher's Exact test highlighting difference in rain occurrence at Vagar, Faroe Islands. See Appendix 2 for weather data.

A)	t	df	p-value	Significance
Mean Temperature	2.4761	209.25	0.01408	**
Mean Wind Speed	1.2596	239.82	0.209	
B)	Fisher's Exact Test		p-value	
Rain Occurrence	NA	NA	0.3574	

Appendix 4. Monthly NAO Index from August to November for 2022 and 2023.

	2022	2023
August	+1.47	-1.16
September	-1.61	-0.44
October	-0.72	-2.03
November	+0.69	-0.32

