

Environmental correlates of early-life growth, natural selection, and components of phenotypic variation in a long-term experimental study system of black-legged kittiwakes

by

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A thesis submitted to the Department of Biology

In conformity with the requirements for

the degree of Doctor of Philosophy

Queen's University

Kingston, Ontario, Canada

(May, 2023)

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## Abstract

In the face of global environmental change, the ability to predict adaptation has become a priority. To make predictions of adaptation, we must understand how environmental factors shape phenotypic expression, natural selection, and genetic variation. In my dissertation, I explore the effects of natural and experimental environments on phenotypes, selection, and genetic variation using pedigrees, nestling growth traits, and nestling survival data from three long-term seabird monitoring programs. In most chapters, I focus on a Northeastern Pacific population of black-legged kittiwakes *Rissa tridactyla*. First, I review weather conditions' various impacts on nestling avian growth. Next, I use a sliding window approach to analyze three long-term seabird datasets. I use these analyses to identify specific periods of environmental variation that correlate with nestling growth, assess changes in environmental predictors across years, and predict future nestling growth under climate change. My findings reveal specific breeding season periods that are strongly associated with variation in nestling growth. These associations suggest warmer conditions may result in poorer growth for two of the three species studied. Further, windows of environmental influence changed between historical and contemporary periods, emphasizing the need to investigate how such changes might affect adaptation to changing environments. In my final chapters, I use data from a kittiwake food supplementation experiment to examine the relationship between food conditions, the variability of selection strength, and variance components of nestling kittiwake size traits. I find that natural selection is strongest in early ontogeny, in non-food supplemented nestlings, and for the youngest nestlings in a brood. Selection magnitude varied among years, but annual variation in magnitude was similar for all treatment and hatching order groups. Warming conditions have mixed effects on selection that depend on food supplementation and hatching order. Finally, I

use pedigree data to find higher annual variance and evolvability of mass and wing-length in non-food supplemented nestlings, suggesting potential cohort effects and increased evolutionary potential in non-food supplemented nestlings. Together, my results help identify and fill gaps in our understanding of the ability of natural populations to adapt to ongoing climate change.

## Co-Authorship

Chapter 2 is a co-authored review paper:

Sauve, Drew, Vicki L. Friesen (Queen's University), & Anne Charmantier (Université de Montpellier, CNRS). 2021. The effects of weather on avian growth and implications for adaptation to climate change. *Frontiers in Ecology and Evolution* 9: 569741.

Chapter 3 is a co-authored empirical paper:

Sauve, Drew, Anne Charmantier (Université de Montpellier, CNRS), Scott A. Hatch (Institute for Seabird Research), & Vicki L. Friesen (Queen's University). 2022. Environmental conditions variably affect growth across the breeding season in a subarctic seabird. *Oecologia* 198: 307-318.

Chapter 4 is a co-authored empirical paper:

Sauve, Drew, Vicki L. Friesen (Queen's University), Scott A. Hatch (Institute for Seabird Research), Kyle H. Elliott (McGill University), & Anne Charmantier (Université de Montpellier, CNRS). 2023. Shifting environmental predictors of phenotypes under climate change: a case study of growth in high latitude seabirds. *Journal of Avian Biology*, e03062.

Chapter 5 is a co-authored empirical paper

Sauve, Drew, Anne Charmantier (Université de Montpellier, CNRS), Scott A. Hatch (Institute for Seabird Research), & Vicki L. Friesen (Queen's University). 2023. The magnitude of selection on growth varies among years and increases under warming conditions in a subarctic seabird. *Evolution Letters*, in press.

Chapter 6 is a co-authored empirical paper in preparation for Evolution.

Sauve, D., Vicki L. Friesen (Queen's University), Scott A. Hatch (Institute for Seabird Research), & Anne Charmantier (Université de Montpellier, CNRS). 2023.

## Acknowledgements

I am beyond grateful for my advisors and mentors, Vicki Friesen and Anne Charmantier. I have worked with Vicki for almost a decade, and it is due to her long-standing support that I have been able to finish this thesis and countless other successes. Vicki's support, guidance, and insight have shaped my approach to science and given me space to grow into a confident scientist. Anne welcomed me warmly into the CEFE department and introduced me to a new scientific environment and set of colleagues. Anne's leadership, excitement for science, and strategic guidance are all attributes I look up to and hope I can exemplify in the future. I feel fortunate to have worked with not one but two incredible scientists – I honestly cannot express the numerous ways that I am thankful to Vicki and Anne for their mentorship.

Thank you to all the Middleton Island field teams who collected data year after year to build and maintain such a valuable seabird monitoring field station. Massive thanks to Scott Hatch, Shannon Whelan, and Kyle Elliott for scientific guidance and assistance and opportunities to conduct field work on Middleton. Thank you to Abraham Turner, Anne Mouillier, Catherine Lee-Zuck, Dan Netti, Emily Choy, Ethan Hermer, Fred Tremblay, Hannes Schraft, Hanah Weipert, Josh Cunningham, Kristen Lalla, Mae Lacey, Martha Hatch, Sierra Pete, and Sydney Collins for some wonderful field seasons on Middleton. Finally, thank you to Amélie Fargevieille, Hélène Dion-Phénix, and Claire Doutrelant for allowing this at times clumsy seabird researcher to help with mésange data collection in Pirio, Miro, and La Rouviere. I never imagined that I would have the opportunity to work on Islands in numerous oceans and the Mediterranean Sea! I acknowledge that Queen's University is situated on Anishinaabe and Haudenosaunee territory, research on Middleton Island is conducted on Chugach and Eyak territory and research on Coats Island is conducted on Inuit Nunangat. We are grateful to be able to conduct research on these lands.

Thank you to Queen's University, NSERC, TD Bank, Polar Knowledge Canada, and the Institute for Seabird Research for logistical and financial support. Thank you to the many Queen's graduate students and Friesen lab members who I learned from and enjoyed many Fridays at the grad club with:

Anna Tigano, Cat Dale, Nick Cairns, Becky Taylor, Bronwyn Harkness, Brody Crosby, Ciccio Schioppa, Dave Ensing, Chris Boccia, Alisa Samuelson, Haley Kenyon, Katherine Moir, Cale Gushulak, Ryan Franckowiak, Debbie Leigh, Heather Lounder, Jihyun Kim, Charlotte Ngo, Shayla Kroeze, Tim Birt, Gihyun Yoo, Ying Chen, Lila-Colston Nepali, Katie Birchard, Ferris Nowlan, Hayley Turcotte, and Dominique Charland. Thank you to Maria-José, a wonderful co-instructor for Biology 206; I am very grateful that my first lecturing experience was with someone so organized and skilled at teaching! Thank you to my friends Alexa Peng, TJ Bryce, Mikhail Hayhoe, Ethan Munro, Zach Dravis, Alp Aydinoglu, and Alex Bartsch for keeping me grounded.

Thank you to my Dad, Michael Sauve, for getting me excited about science and the natural world. Thank you to my soon-to-be family-in-law Hilary Clarke, Arthur Mitchell, Neil Belmore, and Jessica Murray. I am very thankful for all the love and support you have provided. Finally, I am thankful to my mom, Julia Davidson, who worked harder than anyone I know throughout her life to support my siblings and me – I know you would have been very proud.

Finally, thank you to Kate Belmore for everything. You have been a constant and unwavering source of support.

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## List of Abbreviations

<i>A</i>	asymptote or maximum size reached during growth in grams
Alpha	first-hatched nestling
AICc	second-order estimate of Akaike information criterion
AVHRR	advanced very high-resolution radiometer
Bayes R <sup>2</sup>	bayesian coefficient of determination
<i>b<sub>A</sub></i>	vector of the fixed effects specific to the asymptote
Beta	Second-hatched nestling
<i>b<sub>k</sub></i>	vector of the fixed effects specific to the maximum growth rate
<i>b<sub>T</sub></i>	vector of the fixed effects specific to the timing of maximum growth
<i>d</i>	shape parameter of the growth curve (sigmoid when greater than 0)
$\varepsilon$	vector of the residual effects
GAM	general additive model
<i>h</i> <sup>2</sup>	narrow sense heritability
<i>I</i>	vector of individual effects
<i>k</i>	maximum relative growth rate
LOOIC	leave-one-out information criterion
logit	logarithm of the odds $\frac{p}{1-p}$ where <i>p</i> is a probability
<i>n</i>	sample size
NCDC	national climatic data center
NOAA	national oceanic and atmospheric administration
PSIS	pareto-smoothed importance sampling

PDO	Pacific decadal oscillation
RCP	representative concentration pathway
REML	restricted maximum likelihood
SE	standard error
SST	sea-surface temperature
$T$	age in days at maximum growth,
$t$	age in days of a nestling
$V_A$	additive genetic variance
$W$	mass in grams
$X$	a matrix of predictor variables
$Y$	vector of hatch-year effects
$Z_{1-2}$	identity matrices for individual and year effects respectively

# Chapter 1 Introduction

## 1.1 Background

A fundamental issue for evolutionary ecologists is predicting how phenotypes will respond to environmental change in natural populations (Merilä et al. 2001; Pujol et al. 2018). Why is it so challenging to predict trait changes (and [mal]adaptation) in wild populations compared to lab or agricultural populations? One of the main complications for prediction arises from the interactions of biotic and abiotic environments that a population experiences. Quantitative genetics is built around a predictive framework for phenotypic change, but the challenge, particularly for wild populations, is in measuring and including several key variables in this framework, such as plasticity; temporally or spatially varying selection; and changes in the genetic and environmental variances of a trait (Price 1970; Endler 1986; Price et al. 1988; Hoffmann and Sgrò 2011; Queller 2017; Cattau et al. 2018; Hajduk et al. 2020; Villemereuil et al. 2020). My thesis aims to explore the complex role that the environment can have on phenotypes, selection, and variation in phenotypes using observational data from three long-term studies of seabird populations.

Humans have always been interested in the phenotypes of the wild populations around them. For example, the phenology of cherry blossoms has been recorded for centuries, seabird eggs with rare or interesting colour patterns have been collected and examined for decades (Aono 2015; Birkhead et al. 2021), and in the present day, millions of users document millions of observations on websites like iNaturalist (<https://www.inaturalist.org>). We (humans and especially biologists) are curious about phenotypic variation: why does that plant, animal, or fungus have that particular form, and why don't all individuals or populations have it? We also

use phenotypes to indicate that the environment is changing and causing a response in a population. For example, antimicrobial resistance in *E. coli* indicates antimicrobial overuse, and the phenology of wild populations is used to indicate climate driven changes in ecosystems (United Nations Environment Program 2017, 2022).

For decades and sometimes even centuries, biologists and dedicated record keepers have been collecting data that can help us predict phenotypic change in response to changing environmental conditions (Hall and Hall 1988; Aono 2015). All this data is an immense wealth of knowledge on phenotypes that ranges from observations and descriptions of phenotypes in particular environments to experimental manipulations of environmental or genetic conditions to induce phenotypic change. Observational environment-phenotype correlations are significant as they provide our first expectation for phenotypic change in a particular environment. For example, because red deer *Cervus elaphus* have earlier calving dates and lighter calves under warmer temperatures, we expect earlier calving dates and lighter calves in future warmer conditions (Froy et al. 2019). These observed responses allow initial predictions and prompt the development of hypotheses regarding processes underlying these environment-phenotype links.

Often the major scientific challenge begins after the identification of an environment-phenotype relationship. Follow-up statistical or experimental work can then provide evidence for the causes of phenotypic variation. For example, structural equation modelling provided evidence that in big horn sheep, *Ovis canadensis*, colder spring temperatures cause lower body condition, resulting in later moult (Larue et al. 2022). Similarly, experimental work suggests that pollen colour variation in trout lily *Erythronium americanum* is likely caused by regional pollinator preference (Austen et al. 2018). These follow-up studies are incredibly important because they provide nuance to initially simple predictions. This nuance is important for two

reasons: 1) it allows us to make better predictions, and 2) it leads us closer to a mechanism for trait change. For example, in the superb fairy-wren *Malurus cyaneus* understanding that warmer temperatures prior to breeding can increase nestling size while warmer temperatures during breeding can decrease nestling size allows us to make predictions for years with various combinations of warm and cool seasons (Kruuk et al. 2015a). Understanding this season-specific effect also suggests that pre-breeding impact on parents or a lagged effect on food resources can cause changes in body size. Specificity can narrow our focus so that we can apply more intensive experimentation or statistical tools to get closer to the cause of the variation in a particular phenotype.

Finally, to make evolutionary predictions under environmental change, we need to know how the environment alters the two major components of an evolutionary response: 1) selection on traits (and trait responses); and 2) the genetic variance of traits. The major challenge in acquiring this information is that the target of selection is often unknown, and it has proven challenging to generalize about how changing environmental conditions in natural settings will alter selection and genetic variation (Charmantier and Garant 2005; Wood and Brodie 2015; Pujol et al. 2018; Walsh and Lynch 2018). Long-term studies where phenotypes and fitness of relatives are measured across varying environmental conditions are now enabling us to gather this information (Gienapp and Brommer 2014). The longevity of these datasets constantly provides new information, and the advancement of scientific tools and theory are providing answers to problems related to exactly how the environment and genotype of organisms interact to produce phenotypes (Chevin et al. 2015; Gienapp et al. 2017; Villemereuil et al. 2020; Hunter et al. 2022).

Early life is often a strong selective period: environmental effects during early-life can have a large impact on phenotypes, and body size is a trait commonly under positive directional selection (Kingsolver and Diamond 2011). In wild populations, much of the work on phenotypic responses to climate change has focused on changes in the timing of life-history events (e.g. egg-laying date) (Vedder et al. 2013; Radchuk et al. 2019). Offspring growth is often associated with subsequent survival and recruitment, and early life experiences are known to impact adult phenotypes (Perrins et al. 1973; Weinig and Delph 2001; English et al. 2016; Merrill and Grindstaff 2018). Organismal growth has been studied for a long time (Medawar 1941). However, changes in predation, competitors, temperature, and nutrition associated with climate change are expected to impact the growth and size of organisms (Dmitriew 2011; Sheridan and Bickford 2011; Kruuk et al. 2015*b*; Naya et al. 2017; Prokosch et al. 2019). A challenge in measuring the response of growth to climate change is identifying critical environmental influences or cues on growth (Bonamour et al. 2019).

## **1.2 The Study Systems**

My thesis uses long-term data sets on nestling growth for three Arctic and subarctic seabird species. Black-legged kittiwakes *Rissa tridactyla* are the main studied species in this thesis, but thick-billed murres (*Uria lomvia*) and glaucous-winged gulls (*Larus glaucescens*) are included in the fourth chapter. Black-legged kittiwakes are cliff-nesting pelagic gulls that are widely distributed across the marine Holarctic realm (Hatch et al. 2020). Because of their tendency to build nests on human infrastructure they have been widely studied by seabird biologists for decades (Coulson and Thomas 1985). Black-legged kittiwakes are long-lived and have a high degree of nest-site fidelity and very low rates of extra-pair paternity. These attributes enable researchers to repeatedly measure birds each year and build an accurate pedigree from banding

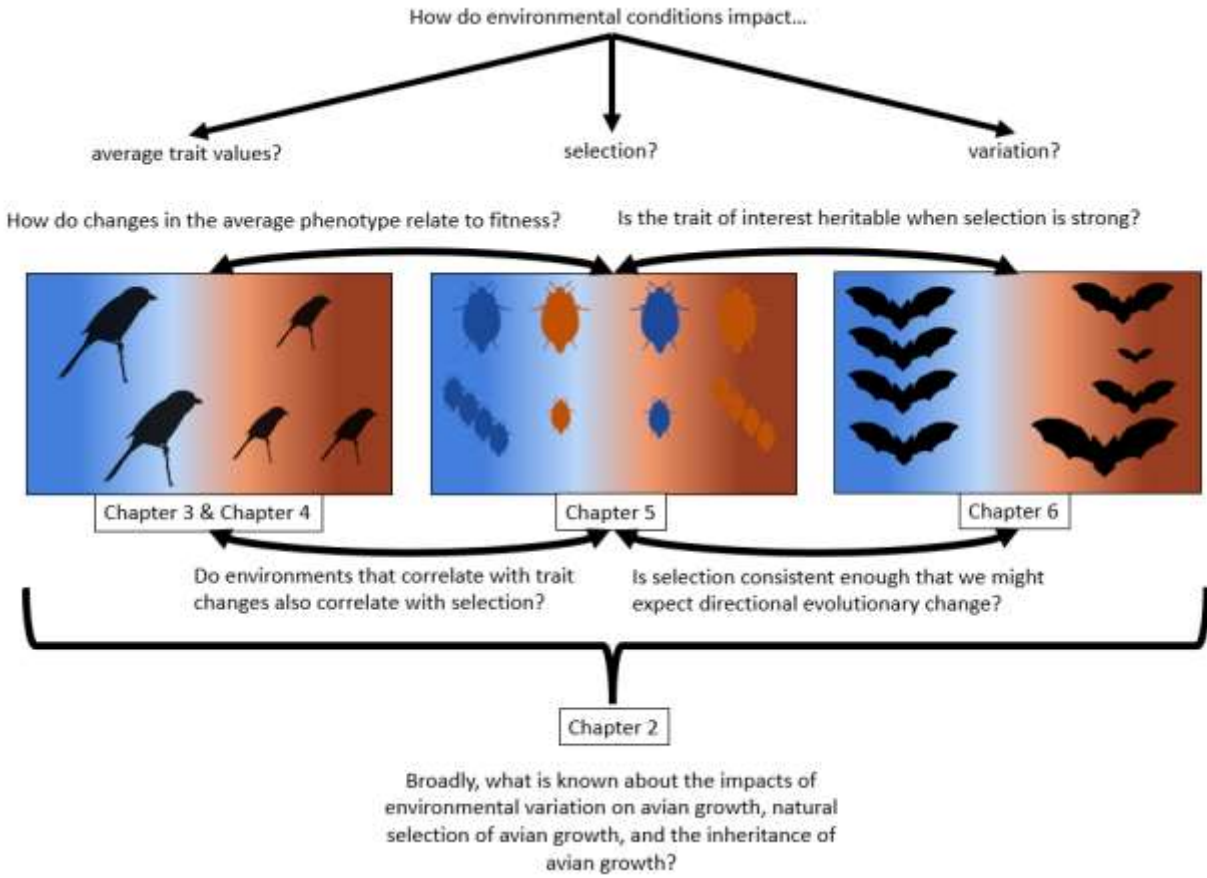
data (Helfenstein et al. 2004; Hatch et al. 2020). Further, adults are long-lived, with an adult life expectancy of 13 years (Hatch et al. 1993). The species' longevity allows us to observe the expression of multiple breeding phenotypes across variable environmental conditions from year to year. Our study site on Middleton Island is particularly valuable because of an ongoing food-supplementation experiment that allows comparison of a food rich and food poor environment (Hatch 2013). As changes in food resources are expected to be a major contributor to changes in the phenotypic expression and natural selection of traits under climate change (Durant et al. 2007), this experiment provides valuable contrasts for making predictions about climate change and resource altered environments.

### **1.3 Research Questions**

In my thesis, I aim to improve our understanding of how environmental conditions alter phenotypes in wild conditions. Because I am motivated to study this problem in the context of climate change, most of my thesis chapters are focused on understanding how changing climatic conditions might affect adaptation. However, the results are often generalizable to the impacts that gradually changing, heterogenous, or fluctuating environments might have on adaptation. In chapter 2, I review the impacts of weather conditions on avian growth and nestling morphology. In chapter 3, I test the hypothesis that early breeding season conditions impact traits expressed earlier in ontogeny more than traits expressed later in ontogeny. In chapter 4, I evaluate whether environmental predictors of growth remain consistent over time. In chapter 5, I examine the link between selection, feeding regime, and warming conditions. Finally, in chapter 6, I evaluate the impacts of experimentally manipulated food conditions on the genetic and environmental components of phenotypic variance. Combined, these chapters evaluate the different environmental influences that could affect a phenotype (Fig. 1.1).

## **1.4 Significance**

Understanding whether climate change will result in evolutionary change depends on understanding how changing environments shape natural selection acting on phenotypes in wild populations. Selection drives phenotypic change and adaptation. Measuring selection is required to understand whether a plastic response is adaptive or to predict the evolutionary response of a trait. The environment during early life can impact the phenotypic expression of a trait in later life (Moore and Martin 2019). Therefore, the fitness consequences of a trait may not become apparent until we consider fitness at all life stages. To make predictions, we need to measure selection, but understand how and why it fluctuates among years. Researchers working on phenological traits have begun to measure variation in selection and link it to environmental conditions (Chevin et al. 2015; Gamelon et al. 2018; Vilmereuil et al. 2020), and it will be valuable to gather this information for early-life morphological and growth traits. Further, because the amount of phenotypic variation within a population can affect ecological and evolutionary dynamics, understanding how this variation changes in response to environmental change is crucial for predicting the impacts of rapid global change on population dynamics (Sultan 2015; Wood and Brodie 2015; Cressler et al. 2017). One key area of interest is how additive genetic variation changes in response to changes in the environment, as this can lead to adaptive genetic change between generations (Falconer and Mackay 1996; Hoffmann and Merilä 1999; Hoffmann and Sgrò 2011).



**Figure 1.1: Relationships among thesis chapters and major questions asked in the dissertation.**

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## **Chapter 2 The effects of weather on avian growth and implications for adaptation to climate change**

### **2.1 Abstract**

Climate change is forecasted to generate a range of evolutionary changes and plastic responses. One important aspect of avian responses to climate change is how weather conditions may change nestling growth and development. Early-life growth is sensitive to environmental effects and can potentially have long-lasting effects on adult phenotypes and fitness. A detailed understanding of both how and when weather conditions affect the entire growth trajectory of a nestling may help predict population changes in phenotypes and demography under climate change. This review covers three main topics on the impacts of weather variation (air temperature, rainfall, wind speed, solar radiation) on nestling growth. Firstly, we highlight why understanding the effects of weather on nestling growth might be important in understanding adaptation to, and population persistence in, environments altered by climate change. Secondly, we review the documented effects of weather variation on nestling growth curves. We investigate both altricial and precocial species, but we found a limited number of studies on precocial species in the wild. Increasing temperatures and rainfall have mixed effects on nestling growth, while increasing windspeeds tend to have negative impacts on the growth rate of open cup nesting species. Thirdly, we discuss how weather variation might affect the evolution of nestling growth traits and suggest that more estimates of the inheritance of and selection acting on growth traits in natural settings are needed to make evolutionary predictions. We suggest that predictions will be improved by considering concurrently changing selection pressures like urbanization. The importance of adaptive plastic or evolutionary changes in growth may depend

on where a species or population is located geographically and the species' life-history. Detailed characterization of the effects of weather on growth patterns will help answer whether variation in avian growth frequently plays a role in adaptation to climate change.

## **2.2 Introduction**

Avian growth can affect fledgling survival and recruitment, and early-life experiences are known to impact adult phenotypes (Haywood and Perrins, 1992; Lindström, 1999; Maness and Anderson 2013; Merrill and Grindstaff, 2018). Given gradual warming and increasingly stochastic weather conditions under climate change, some growth strategies might result in higher fitness than others. Therefore, predicting future changes in fitness and demography under climate change could depend on understanding the effects of current weather variation on offspring growth. The consequences of weather variation on offspring development will likely be complex and will, to some degree, depend on a species' life-history and ecological niche.

Growth patterns in birds vary, and differences among populations may be adaptations to their local environments (Ricklefs, 1968; Emlen et al., 1991; Starck and Ricklefs, 1998). Global patterns of variation in avian growth within species can generate hypotheses for how the changing climate will influence growth-related traits. For example, given the observation that individuals tend to be smaller in warmer habitats both within and across species (Bergmann's Rule; Bergmann 1847 as cited in Salewski and Watt 2017) we might predict that for a given species, natural selection will favour nestlings that fledge at a smaller size in a warmer climate (Millien et al., 2006). Introduced House Sparrows *Passer domesticus* in North America and Australia both exemplify predictions from Bergmann's rule: birds in the colder regions of both continents are on average larger (Johnston and Selander 1964, 1973; Andrew et al., 2018). Clines in body size could be driven by natural selection, developmental constraints, or both (Fleischer

and Johnston 1984; Andrew et al., 2018). Effects on size during development are important because many bird species approach their final structural size before fledging, meaning there may be little opportunity for compensation later in life (Gill and Prum 2019).

Plastic adjustment of growth could allow rapid adaptation to changing conditions, but evolution of growth traits might be required if current environmental cues no longer predict future environments. To predict possible phenotypic changes in nestling growth we need to understand how weather variation affects nestling growth, how new weather conditions under climate change are changing the selection on avian growth traits, and the additive genetic and environmental variance of growth traits. Some studies have identified carry-over effects of growth on adult fitness with larger sizes being correlated to increased and decreased fitness (Gardner et al., 2011; Teplitsky and Millien, 2014; van Gils et al., 2016), but few studies examine whether patterns in growth are adaptive or maladaptive. Examining growth-environment relationships jointly with patterns of genetic change is important because phenotypic plasticity can mask evolutionary change (Merilä et al., 2001; Bonnet et al., 2017; Dobson et al., 2017), and plastic responses can contribute to an adaptive or maladaptive response to changing weather conditions (Ghalambor et al., 2007; Snell-Rood et al., 2018). An essential aspect of studying growth is to quantify it in a way that allows among population, individual and genetic variation to be estimated (Box 1).

In this review, we **1)** highlight why studying weather-related changes in avian growth might be important to understand avian responses to climate change, **2)** review the currently documented effects of weather on avian growth in wild populations, and **3)** highlight that understanding the selection operating on growth traits and the inheritance of growth traits is needed to predict future phenotypic responses. We define weather as local within-year variation

in temperature (of air and sea surface), solar radiation, precipitation and wind, and climate as the average weather across multiple years for a given region. We explore the effects of minimum, maximum, average, and duration (heatwaves, rainfall) of weather variables.

### 2.3 Box 1 - Methods for quantifying growth

Avian growth can be investigated using a broad range of traits and different statistical modelling approaches. Often, measurements of size or shape near fledging are used because these are more comparable across studies and can predict post-fledging survival (Maness and Anderson 2013). However, single time point measurements can hide variation in growth among individuals if individuals follow different trajectories to the same final size (Fig 2.1).

Repeated measurements made throughout nestling development can be used to fit a curve to the data as a function of age. For growth data, logistic models are often used, and the model's **asymptote**, **maximum relative growth rate**, and **timing of maximum growth** may be estimated as biological parameters of interest describing growth (Fig 2.1; Fig 2.2A; Tjørve and Tjørve, 2010; Aldredge, 2016). The unified family of growth models proposed by Tjørve and Tjørve (2017, 2010) allows flexible, comparable, and biologically interpretable estimates from various growth model families. Biologically, the **asymptote** should provide an estimate of the maximum size reached by a nestling. However, the **asymptote** in many models may not be a good indication of a nestling's fledging mass, as a nestling could fledge before the maximum mass is reached, or in some avian species nestlings reach an asymptote and then decline in mass before fledging.

Such *function-valued trait approaches* summarize the growth trajectory and enable researchers to explore whether different environments affect the growth rate, timing, or size of a nestling. Linear and polynomial functions could also be used, with the terms of the polynomial

being treated as the parameters of interest. Instead of fitting functions to a growth trajectory, sometimes the average difference between consecutive daily measurements (e.g. Peck et al., 2004; Harter, 2007; Divoky et al., 2015) or the daily deviation from growth in ideal conditions are used as an indication of daily growth (Keller and Noordwijk 1993).

*Character-state models* provide a flexible method for modelling growth, where one can estimate age-specific measurements as separate, yet correlated traits (Roff and Wilson, 2014; Fig 2.2B). Note that character-state and polynomial functions are equivalent in many situations. In a character-state approach covariances among age-specific masses can be fitted across all ages, or be restricted to consecutive ages only, in what is called an “ante-dependence” model (see the supplemental material of Hadfield et al., 2013 and Thomson et al., 2017; Hadfield, 2019). Both function-valued trait and character state approaches to modelling growth are identical to models that measure trait plasticity across environments, but replace environmental variation with age (Falconer, 1952; Via and Lande, 1985; Jong, 1990; Gavrillets and Scheiner, 1993; Chevin et al., 2013). Function-valued trait approaches can perform poorly if individuals or genotypes have different curve shapes and can be harder to interpret biologically (Roff and Wilson, 2014). Generally, function-valued trait approaches use fewer parameters. Therefore, when sufficient data are available, comparison of function-valued and character-state approaches might be valuable in determining when during ontogeny function-valued trait approaches are not capturing variation during growth (Morrissey and Liefting 2016). If a linear model is used, environmental effects on the slope or intercept of the line could be detected, yet a gain or loss of mass at any specific time during growth, which could be biologically important, would be difficult or impossible to detect. A character-state might be better able to determine *when* during ontogeny the environment affects a trait. Houslay (2017) provides accessible tutorials implemented in the

R package MCMCglmm for both character state and function-valued trait approaches that could be used to model avian growth (Hadfield, 2010).

Function-valued trait and character-state approaches can be analyzed in a mixed model framework, so that hierarchical (co)variances are estimated (function-valued trait approach, Aldredge, 2016; character-state approach, Thomson et al., 2017). Further, Bayesian models now allow the fitting of flexible models that can estimate the fixed effects of weather and environmental variation on specific parameters or age-specific traits in a single model (Hadfield, 2010; Bürkner, 2017).

## **2.4 Importance of studying weather-related changes in avian growth**

Understanding weather-related changes in avian growth is important for two reasons: some individuals or genotypes might survive better than others in stressful weather conditions, and weather variation may change a population's demography through influences on nestling traits.

### **2.4.1 Plasticity of avian growth and development**

Individuals differ in their growth because of genetic, environmental, and parental effects.

Understanding the causes of these growth differences is important because some individuals may have higher fitness under changing conditions (Kruuk, 2004; Wilson et al., 2010). In theory, the same individual or genotype could also produce several different phenotypes given different weather conditions (phenotypic plasticity), and the plasticity of an individual's phenotype could also vary among individuals because of genetic, permanent environmental, or parental effects.

Plastic changes have gained recognition as common responses to changing environmental conditions (Ghalambor et al., 2007; Charmantier and Gienapp, 2014; Snell-Rood et al., 2018).

Central questions in evolutionary ecology are **1)** whether plasticity will allow adaptation to new weather conditions, and **2)** how plasticity might affect the rate of evolutionary change.

Studying the plasticity of avian growth requires the estimation of how growth patterns can change for a given individual (or a given genotype) across different environments. Such measures are impossible at the individual-level because a bird only grows once. However, in long-lived and philopatric species, associations between growth and weather variation may be likely to result from plastic rather than evolutionary responses because the population genetic background may change little from one year to another. In a wild setting, a cross-fostering experiment across a weather gradient (experimental or natural) may reveal if different families have on average different or similar growth patterns across environments (for a discussion on artificial breeding designs, see Roff and Wilson 2014). To our knowledge, no studies have analyzed cross-fostering in wild birds, with the goal of measuring differences among families in changes in growth patterns across weather gradients.

Because a proportion of the variation in growth traits is determined by parental behaviour, we might be able to measure the plasticity of nestling growth by considering nestling growth traits as parental traits in species where faithful pairs repeatedly reproduce (Lloyd and Martin, 2004; Wilson et al., 2005). Nestling growth traits that are measured across years for parents can then be considered repeated measures of a parental trait. We can then try to examine the plasticity of the parental care contribution to nestling growth by examining how nestling growth traits vary across environments for a given parent or pair of parents. Importantly, because reproductive investment is a complex function of age and parental condition, such a model will require careful consideration of parental age or breeding experience (McCleery et al., 2008) and the weather conditions parents experience. Consequently, informing such a model will likely require large sample sizes but will provide valuable information on the suite of growth responses individual parents or parental genotypes could generate.

One of the challenges in studying plastic responses in wild populations is determining the environmental variable to which an organism responds (Scheiner, 1993; Gienapp and Brommer, 2014). This problem is further complicated because a trait could be affected by multiple weather variables, interacting weather variables, or even the same weather variables in different ways at different times throughout ontogeny (Fig 2.3). Recent statistical techniques try to address the difficulty of identifying time windows of weather variation that affect a trait of interest (van de Pol et al., 2016). The van de Pol et al. (2016) method is an exploratory approach that compares multiple windows within a period of time (relative to the biological variable or an absolute time frame) to determine those that best predict (relative to all windows examined) the trait of interest. To understand when during the breeding season weather affects nestling growth, it may be useful to explore weather variation within the prelaying, prenatal, and growth stages (Fig 2.3). Importantly, we mainly discuss physical growth in this review, but many of the impacts of weather also affect the development (e.g. cognition, thermoregulation, motor function) of nestlings. Understanding how and when during the breeding season development is affected by weather is an additional complexity that will be important to study for a more complete understanding of the impacts of weather.

In the context of growth and development, identifying environmental correlates may still be challenging because weather variation among prelaying, prenatal, and postnatal periods might be tightly correlated - making it difficult to disentangle during which period weather variation affects a trait. For more easily manipulated weather effects like temperature, experimental work may allow researchers to measure the effects of different time windows by manipulating temperature during specific time periods (Andreasson et al. 2020; Andreasson et al., 2018; Andrews et al., 2017; Fig 2.3). Exploring effects of weather variation outside the breeding season

will be valuable if weather patterns are expected to have long-term effects on the resources available or the condition of parents during the breeding season. Understanding the environmental cues that affect the expression of a character is essential because plasticity might allow persistence in the face of changing weather conditions (Vedder et al., 2013), but could also increase the speed of extinction if cues are no longer informative (Reed et al., 2010). Further, in seabirds, nestling growth is routinely used as an indicator of environmental conditions (Cairns, 1988). Inferences from such traits require an intimate understanding of the relationship between environmental variation and the measured biological trait (Grémillet and Charmantier, 2010; Brisson-Curadeau et al., 2017).

#### **2.4.2 Nestling Growth and demography**

Weather effects on nestling traits can also affect the demographics of bird populations (Bryant, 1978; Salaberria et al., 2014). In many avian species, growth is likely to affect survival to fledging (nestling survival) and post-fledging survival (juvenile survival). In a review of predictors of juvenile survival, Maness and Anderson (2013) found (in a subset of quality-controlled studies) that nine out of ten studies identify an effect of nestling mass on juvenile survival, but noted that few studies assess whether growth rates affected juvenile survival. Given evidence that growth traits can influence nestling and juvenile survival (Maness and Anderson 2013), the effects of variation in growth caused by weather patterns might most strongly affect demography in short-lived bird species (Saether and Bakke 2000). However, if nestling growth traits determine adult survival or fecundity, weather-induced nestling variation might change the demography of a broad range of avian species. During early-life, environmental conditions, like weather, are expected to play a role in shaping adult phenotypes and fitness (Lindström, 1999). A meta-analysis of the effects of early developmental conditions in birds and mammals found that

poor early developmental conditions increases the rate of decline in fecundity with age, but developmental conditions do not influence the age-specific decline in survival in adults (Cooper and Kruuk, 2018). However, the latter result relies heavily on mammal studies, since only one avian study in this meta-analysis investigates the effects of the developmental environment on survival senescence (Hammers et al., 2013). Future studies on birds should investigate the effects of early-life conditions (including weather) on traits expressed in adults.

## **2.5 Documented weather effects on avian growth**

Understanding current responses to weather enables us to extrapolate responses to predict future changes. Here, we review the effects of weather on growth and discuss the different ontogenic pathways through which weather could impact growth (Fig 2.3). To cover studies investigating the effect of weather on nestling growth, we searched in the ISI Web of Science on November 2<sup>nd</sup>, 2020. We used the keywords ‘avian’ OR ‘bird’ + ‘growth’ OR ‘development’ + ‘climate change’ OR ‘global warming’ OR ‘weather’ OR ‘temperature’ OR ‘wind’ OR ‘rainfall’ OR ‘precipitation’ OR ‘sunshine’ OR ‘solar radiation’ OR ‘solar’ OR ‘insolation’ OR ‘experiment’ + ‘offspring’ OR ‘juvenile’ OR ‘nestling,’ which brought up 989 references. We restricted papers to experimental and observational studies that examined the effect of weather variation on nestling growth, leaving 36 studies. Specifically, we retained studies that examined the effect of weather variables (wind, precipitation, solar radiation, temperature, ice- cover, sea-surface temperature) on nestling phenotypes during the growth period. Weather effects identified from our literature search are included in Tables 2.1-2.4.

### **2.5.1 Weather impact of growth through prenatal effects**

In addition to any effects of weather conditions on nestling growth in birds, conditions during embryonic development could affect post-hatching growth. A mother may influence the size of an egg and the hormones in an egg, potentially in response to environmental cues (Love and Williams, 2008; Bentz et al., 2013). The importance of egg size on nestling growth traits is somewhat uncertain. Effects of short-term weather variation on egg size tend to be limited (Nager and Noordwijk 1992; Christians 2002; Thomson and Hadfield 2017; Griffith et al., 2020), and some studies note that egg size affects hatching traits, but this effect deteriorates through ontogeny (Krist, 2011; Williams, 2012).

Weather variation can, but does not always, influence maternal hormones transported into the egg, and these components can affect nestling growth (Schwabl, 1996; Groothuis et al., 2005; Groothuis and Schwabl, 2008; Addison et al., 2008; Ruuskanen et al., 2016). In particular, weather impacts on food may have a strong effect on maternal hormones deposited in the egg and could aid the matching of brood size to environmental conditions (Verboven et al., 2003; Gasparini et al., 2007; Vergauwen et al., 2012; Benowitz-Fredericks et al., 2013; Müller and Groothuis 2013; Merklings et al., 2016). Other than hormonal influences, weather could also indirectly impact nestling growth through antioxidants, immunoglobins and antimicrobial agents (Williams, 2012), but these effects might be more indirect, as these compounds are less likely to affect growth directly and instead likely help nestlings survive in the face of environmental challenges (e.g. parasites).

If weather patterns during the prenatal period can predict the environment that a nestling will develop and grow in, a mother may be able to provide cues or influence the phenotype of her offspring to better match its future environment. However, the extent to which mothers provide such signals, and whether these signals are adaptive, is mostly untested in the wild.

Whether a species has such cues may depend on the predictability of the environment it evolved in, and whether such cues remain adaptive will depend on how the predictability of the environment changes. Parents may even provide auditory cues to their prenatal offspring to signal warm environments resulting, for instance, in lighter 13-day old nestlings in zebra finches *Taeniopygia guttata* (Mariette and Buchanan, 2016).

Predicting changes in growth caused by climate change may depend on knowing the effects of an embryo's thermal environment on the nestling phenotype. Weather can directly affect the thermal environment that avian embryos experience and influence parental incubation behaviour (DuRant et al., 2013; Griffith et al., 2016). Embryo thermal tolerance varies among species, with species from colder climates tending to have broader tolerances and lower optimums (Webb 1987). However, even temperature variation within the range tolerated by an embryo can impact a nestling phenotype (Hepp et al., 2006; DuRant et al., 2010; Nord and Nilsson, 2011).

More experiments warming nest microclimates during incubation on a wide range of species might help clarify the impacts of a warmer incubation environment on nestling growth. Nest microclimate experiments are valuable because they reveal the combined effect of indirect thermal effects on the parents and direct effects on embryos (Table 2.4). Current results from experiments that warm the nest microclimate are variable and different species from the same study location can have contrasting effects on nestling growth (e.g. Mueller et al. 2019; Table 2.4). Few studies have experimentally cooled nests, but those that do find that it decreases nestling size and growth (Table 2.4). A cross-fostering experiment in tree swallows provides an interesting insight because nest warming during incubation increased the early-age mass of nestlings incubated in a warm nest (raised by parents in a control nest) and the late-age mass of

nestlings incubated in a control nest but raised by parents from a warm nest (Pérez et al. 2008). The cross-fostering experiment suggests carry-over effects of warming on parental care during growth and direct benefits of warming on young nestlings.

### **2.5.2 Post-hatching weather effects on avian growth**

Variation in weather during the growth period is likely to affect chicks both directly and indirectly. Growth can be influenced by changes in thermal environments (e.g. McKinnon et al., 2013; Cunningham et al., 2013; Tables 2.1 & 2.4), and changes in food availability and parental care (e.g. Keller and Noordwijk 1994). Scientists have long been interested in the effects of weather on growth and both historical and recent studies provide a baseline for making qualitative and quantitative predictions for changes in growth under different weather conditions (Lack and Lack 1951; Hawksley 1957; Tables 2.1-2.4). Predicting how climate change will impact avian growth depends on understanding how nestlings are affected by different weather components and how these weather components are expected to change under climate change.

### **2.5.3 A warmer growing environment can positively or negatively impact nestling growth**

Average global temperatures are expected to continue to increase with climate change, and for many regions, the frequency of heatwaves and variability of thermal environments are expected to increase (Intergovernmental Panel on Climate Change 2018). Increasing temperatures can result in either challenging or improved growing conditions for nestlings and can operate either directly through thermal changes experienced by nestlings or indirectly by affecting parents' foraging or brooding behaviour (Andreasson et al. 2020; Table 2.1; Fig 2.3). The effects of warming may vary among species, populations, and environments because some populations may be closer to their thermal limits or may be more susceptible to dehydration. For example,

species living in environments below their thermal optimum may benefit from increased natural air temperatures during development (e.g. McKinnon et al., 2013), while increased air temperatures or heatwaves may have strong negative impacts on species living close to their thermal limits (Conradie et al., 2019). The effect of thermal changes depends on the ability of nestlings to thermoregulate. If temperatures are beyond a nestling's thermal neutral zone (the temperature range that body temperature is maintained with little energy expenditure), nestlings will have inefficient physiological processes unless they allocate energy to thermoregulation. Further, nestlings might use limited energy resources on thermoregulation, instead of growth, to prevent body temperatures outside their thermal maximum (e.g., Andreasson et al., 2018).

In many bird species, warmer temperatures are associated with faster growth, heavier asymptotes, heavier age-specific masses, or have no effects at all (Dyrce 1974; Hiraldo et al., 1990; McCarty and Winkler, 1999; see Table 2.1). But, warming temperatures can also correlate with slower avian growth and smaller nestlings. In a population of blue tits in Lancashire in the UK, warmer air temperatures correlate with slower increases of tarsus length, head size, feather length, and body mass (Mainwaring and Hartley, 2016), and in nestling Eastern kingbirds *Tyrannus tyrannus* high temperatures covary with smaller age-specific masses (Murphy 1985). Similarly, in arid environments, warmer temperatures correlate with smaller nestlings (Cunningham et al., 2013; Wiley and Ridley, 2016; Andrew et al., 2017; Van de Ven, 2017). In arid environments, warming may frequently approach the thermal maximum of many bird species, resulting in smaller nestlings and increases in nestling mortality either from decreases in parental foraging or direct challenges for nestlings (Cunningham et al., 2013; Wiley and Ridley, 2016; Van de Ven, 2017; Conradie et al., 2019). Studies that experimentally heat passerine nestlings tend to find that warmer conditions slow growth and result in smaller nestlings in warm

climates (Rodriguez and Barba 2016b; Andrew et al. 2017; Table 2.4), but that warmer conditions have a positive or mixed effect on nestling mass and size in cool temperate environments (Dawson et al. 2005; Andreasson et al. 2018; Table 2.4). In many instances, it will be important to explore specific aspects of temperature (e.g. maximum, minimum, mean) because they may affect growth differently (Table 2.1). For example, crimson rosella *Platycercus elegans* nestlings are heavier when the minimum nest temperature is high, but nestlings are lighter when the mean nest temperature is high (Larson et al., 2015). Finally, birds that produce several broods could face different weather conditions for each brood. For example, because temperatures are warmer when spotless starlings *Sturnus unicolor* produce their second brood, increasing temperatures result in smaller 14-day old nestlings, while the opposite effect is found for first broods (Salaberria et al., 2014). Different temperature regimes during early and late broods suggest nestlings in late broods might be more strongly impacted by warming conditions unless parents can adjust nesting locations (presumably to cooler locations) for their second broods.

#### **2.5.4 Sensitivity to thermal variation could vary throughout nestling ontogeny**

To understand the impacts of temperature variation, we also need to investigate the potentially varying impacts of a thermal challenge during different time points in ontogeny. Therefore, to predict warming effects on growth patterns it may be important to identify periods of weather within a season that might impact growth and determine how these time periods are predicted to change.

Development of thermoregulation varies among species, but endothermy develops after hatching in birds and earlier during ontogeny in precocial species than in altricial species (Dunn, 1975; Whittow and Tazawa, 1991; Nichelmann and Tzschentke, 2002; Price and Dzialowski,

2018). Because of better thermoregulatory abilities, young precocial nestlings may be better able to survive temperature challenges than young altricial species (Hohtola and Visser 1998). Within a species, mass is an important determinant of thermoregulatory ability (Visser 1998), but most studies investigate relationships between size and thermoregulation among species and it is unknown how this relates to variation among nestlings within a species. In the context of a warming environment, smaller birds could be better able to cope with heat stress through faster evaporative cooling (McKechnie and Wolf, 2010), but evaporative cooling causes water loss, leaving small birds vulnerable to dehydration (Whitfield et al., 2015). Consequently, small nestlings may be more susceptible to high temperatures in water-limited environments than large nestlings because of potential dehydration (Whitfield et al., 2015). However, many small birds that live in hot and arid environments will have adaptive strategies, like facultative hyperthermia, that allow tolerance of challenging high temperatures (Gerson et al. 2019; Freeman et al., 2020).

To predict the effects of a warming environment on avian growth, it will be important to know whether hot temperatures during early life can improve tolerance of warmer environments later in life. Evidence from poultry suggests temperature conditioning during incubation and early ages can improve growth performance in warm and cold environments (Nichelmann and Tzschentke, 2002; Shinder et al. 2002; Loyau et al. 2015; Oke et al., 2020; reviewed in Nord and Giroud 2020). No study has investigated the effects of short-term prenatal exposure to hot or cold temperatures in wild birds, but continuous exposure to low incubation temperatures generally reduces a nestling's thermal regulatory ability (reviewed in Nord and Giroud 2020).

### **2.5.5 How does adult thermoregulation relate to offspring thermoregulation?**

According to the 'climate variability hypothesis,' high latitude birds may be better able to tolerate temperature variation (Stevens, 1989). This hypothesis suggests that organisms that

experience more variable climates should have wider thermal tolerances, and climate variation tends to increase with latitude (Stevens, 1989). A meta-analysis of non-migratory birds supports the climate variability hypothesis - adults of bird species living in variable environments can tolerate a broader range of temperatures (Khaliq et al., 2014). Importantly, migratory bird species do not demonstrate a trend towards increased or decreased tolerance to environmental conditions with latitude (Khaliq et al., 2014). However, when trying to predict the impacts of weather changes on bird species, the variability of the environments where the species evolved may be important. Given this empirical result on adults, we might predict that the offspring of species adapted to more variable environments can tolerate more warming. Note, however, that the relevance of tolerance in adults depends on how tolerance of offspring is related to adult tolerance. If offspring have broader or narrower thermal niches than adults, they may have better or worse resilience than adults to direct effects of temperature challenges. No studies of wild birds have measured thermal tolerance development and compared it to adult birds' thermal tolerance (Nord and Giroud 2020).

### **2.5.6 Weather impacts growth through changes in food availability**

Weather variation affects the timing of food abundance, which, depending on when reproduction occurs, can affect the food available for nestling growth (Naef-Daenzer and Keller, 1999; Both et al., 2006; Daunt et al., 2006; Visser et al., 2006). Major components of climate change are shifts in the mean and variability of weather conditions. A consequence of shifting weather conditions is that cues used by birds to time their breeding may become unreliable predictors of food abundance (Bonamour et al., 2019). The mismatch hypothesis suggests that species at lower trophic levels are better able to track shifts in climatic variation than are those at upper trophic levels, resulting in top consumers being less able to time their reproductive events to match food

abundance (Stenseth et al., 2002; Thackeray et al., 2016). Because of changing or variable climatic conditions, many birds may have fewer available food resources while offspring develop. For example, both rainfall changes and an inability to temporarily track shifts in prey species can decrease food availability during nestling growth (e.g., black kites *Milvus migrans* Hiraldo et al., 1990; Lapland longspurs and white crowned sparrows Pérez et al., 2016). In Baird's sandpiper *Calidris bairdii*, increases in asynchrony of hatching date with peak biomass of crane flies (Tipulidae) correlates with a slower maximum growth rate (McKinnon et al., 2012). In thick-billed murre *Uria lomvia*, earlier ice break-up covaries with decreases in Arctic cod *Boreogadus saida* and increases in capelin *Mallotus villosus* in the murre diet. Further, hatching later relative to the ice breakup is associated with smaller 14-day old nestlings (Gaston and Elliott, 2014).

Some avian nestlings demonstrate a remarkable ability to persist under periods of scarce food. Laboratory research and avian husbandry suggest that, in some bird species, nestling growth is incredibly flexible in response to food restriction. Chickens *Gallus gallus domesticus*, Japanese quail *Coturnix japonica*, and mallards *Anas platyrhynchos* raised on restricted diets pause their growth (sometimes for months) then resume typical growth trajectories when food restriction stops, with no evident effect on adult morphology (Jordan, 1953; Singsen et al., 1964; reviewed in Schew and Ricklefs, 1998). Similarly, some seabird species can slow chick growth and delay fledging in years with low food abundance or poor weather conditions (Barrett and Rikardsen, 1992; Weimerskirch et al., 2001; Chiaradia and Nisbet, 2006; Kuepper et al., 2018), and white-fronted bee-eaters *Merops bullockoides* can pause growth during periods of low food availability (Emlen et al., 1991). Some species can maintain growth early in the nestling stage because of spare yolk (Romanoff, 1944), but nestlings may be more vulnerable to food shortages

when the yolk is depleted. For many species, extending growth will not be possible because the time window for breeding is restricted (e.g. many Arctic breeding birds). If the timing of the breeding season is constrained, it may be optimal to mature at a smaller size rather than arrest growth until suitable food sources become available.

### **2.5.7 Life-history strategy may determine how parental care changes under more difficult weather conditions**

Weather can also have indirect effects on growth by influencing the foraging or brooding behaviour of parents (Taylor, 1983; Machmer and Ydenberg, 1990). The degree to which birds can adjust their parental effort is likely to depend on their life-history, possibly resulting in differing magnitudes of impacts of weather variation in species with high versus low adult survival (Ghalambor and Martin, 2001). For instance, under unpredictable or stressful conditions, long-lived species may invest less in reproductive effort, including parental care, with a stronger impact on nestling growth. All species face trade-offs in their allocation of resources into reproduction and survival (Stearns, 1989). These trade-offs may be particularly apparent in altricial species and in species with nestlings dependent on parents for food or thermoregulation. Parents can cope with fewer resources by increasing foraging effort at the expense of their body condition – helping chicks to survive challenging weather conditions. For example, in tree swallows, increases in rainfall correlate with increases in parental provisioning at the expense of declines in adult body condition (Cox et al., 2019). Alternatively, parents may invest less in reproduction during stressful situations to preserve or maintain their body condition. Yellow-nosed albatrosses *Diomedea chlororhynchos* appear to increase provisioning in response to poor nestling condition only if food is plentiful, limiting the costs of reproduction for themselves in unfavourable years (Weimerskirch et al., 2001). Future work could determine

which strategy is adaptive for different life-histories under unpredictable or extreme food conditions.

### **2.5.8 Other components of weather can also affect nestling growth**

Climate change is increasing the frequency of heavy precipitation events (Intergovernmental Panel on Climate Change 2018), and rainfall can have variable effects on avian growth (Table 2.2). The effects of rainfall on nestling growth may depend on when rainfall occurs relative to a species' breeding season (Kruuk et al., 2015). During nestling growth, rainfall can decrease growth rates and age-specific morphometrics (Siikamäki, 1996; Kosicki and Indykiewicz 2011; Kasprzykowski et al., 2014; Pérez et al., 2016; Cox et al., 2019, but see Mainwaring and Hartley 2016; Grzędzicka 2018; Table 2.2). Decreases in growth can result from nestlings having difficulty thermoregulating because of wet downy feathers or difficult foraging conditions for parents (Nye 1964; Keller and Noorwijk 1994). In great tits *Parus major*, days with some rainfall greater than one millimetre result in decreases in daily mass gain by nestlings. The negative association between rainfall and daily mass gain in great tit nestlings is suspected to be caused by decreases in foraging of parents because experimental trapping of adults has negative effects on growth comparable to daily rainfall (Keller and Noordwijk 1994). In hot and dry regions, prey abundance may increase in rainy conditions and will improve foraging conditions for parents and nestling growth rates (Sicurella et al., 2014).

In some studies, rainfall has mixed effects on growth or only impacts nestlings at specific ages. Robinson et al. (2017) categorized three years of their study on Arctic peregrine falcons *Falco peregrinus tundrius* as cool and wet or as warm and dry. In cool and wet years, nestlings grew the fastest, grew to a lower-than-average asymptote, and attained their maximum growth rate at a younger age (Robinson et al., 2017). In little auks *Alle alle*, rainfall during the nestling

period correlates with decreases in the masses of young nestlings, while in red-capped larks *Calandrella cinerea* monthly rainfall has a positive effect on the mass of older nestlings, but no effect on young nestlings (Konarzewski and Taylor, 1989; Ndithia et al., 2017).

In contrast to rainfall during nestling growth, rainfall outside the breeding season might increase avian growth rates and masses because of the generally beneficial effects of rainfall on vegetation and insect abundance. In a population of superb fairy wrens *Malurus cyaneus*, increases in rainfall prior to nestling growth result in heavier nestling masses (Kruuk et al., 2015). Higher rainfall during the nestling stage is associated with increases in gosling size in the Canada goose *Branta canadensis*, but the authors suggest that high rainfall during growth is likely associated with high rainfall prior to the nestling stage (Brook et al., 2015). The authors suggest that disentangling whether rainfall during growth had a negative effect on Canada goose nestling growth might be hard because the observed effect was a combination of earlier rainfall effects on vegetation and direct effects of rainfall on nestling size.

In many regions, global climate change is expected to increase ocean wind speeds but decrease land wind speeds (Torralba et al., 2017). Increases in wind speeds often correlate with lower age-specific nestling masses in seabirds. Common terns *Sterna hirundo*, for example, display reductions in growth when wind speeds are high (Langham, 1968), maybe because of a reduction in the ability of parents to capture prey (Taylor, 1983). Interestingly, high wind speeds do not appear to affect nestling growth of a relative of common terns, sandwich terns *Thalasseus sandvicensis*, perhaps because of differences between these two species in foraging behaviour or morphology (Langham, 1968; Taylor, 1983). In the little auk, wind speed and decreases in visibility correlate with lower masses in nestlings older than five days (Konarzewski and Taylor, 1989). Environmental differences at breeding locations might determine whether a weather

variable impacts growth in black-legged kittiwakes *Rissa tridactyla*: wind speeds do not affect nestlings on a colony in the Gulf of Alaska, but high wind speeds do reduce the growth of nestlings on a colony in the Norwegian Sea (Elliott et al., 2014; Christensen-Dalsgaard et al., 2018). Marine birds may need to change or increase their foraging behaviour with changing weather conditions, or offspring will need to adjust to lower or variable food provisioning.

Components of foraging behaviour in birds can vary among individuals, and individuals may change their behaviour differently in response to weather conditions (Woo et al., 2008; Patrick et al., 2014). Differences among individuals in foraging and how foraging behaviour develops may be essential to determine which strategies are adaptive in an altered environment. Beyond effects on foraging, wind may stress (*e.g.*, via noise) nestlings directly, resulting in altered growth phenotypes (Crino et al., 2020). Evidence from blue tits suggests that increases in wind speeds negatively affect the growth of fourth primary feathers, mass and tarsus, so a decline in average wind speeds on land may result in more favourable growing conditions for some land birds (Table 2.3; but see Sicurella et al., 2014).

Variation in sea-surface temperature is also likely to impact food availability for many seabirds. Average sea-surface temperatures are expected to increase globally, with some regions warming more rapidly than others (Intergovernmental Panel on Climate Change, 2013). Sea-surface temperature changes are likely to affect marine bird species by changing their prey species' distribution, abundance, and phenology, generally resulting in lower food availability and, in extreme cases, in mass seabird die-offs (Piatt et al., 2020). Associations between warm sea-surface temperatures and slower daily mass gain are found in numerous seabird species (Bertram et al., 1991; Hedd et al., 2002; Gjerdrum et al., 2003; Smithers et al., 2003; Peck et al., 2004; Ancona et al., 2011; but see Pinaud et al., 2005). Additionally, sea-ice coverage, age, and

distribution will be important for provisioning in ice-associated seabirds (Gaston and Elliott, 2014; Divoky et al., 2015). Generally, increases in sea-surface temperatures correlate with decreases in nestling masses in seabirds, likely because of low prey availability during breeding.

Lastly, the interaction of different weather effects may change our predictions of future change because interactions among weather variables or other changing variables could enhance or ameliorate negative effects. For example, in a study of barn swallows *Hirundo rustica*, nestling mass between age 8 to 12 days is negatively associated with increasing temperatures, and this effect is stronger during heavier rainfall, but weaker during high wind speeds (Facey et al., 2020).

### **2.5.9 Variation in weather conditions may more strongly impact later-hatching nestlings**

The hatching order of a nestling within a brood might play an important role in how weather interacts with growth. In species with asynchronous hatching, older nestlings can outcompete younger nestlings for food, and younger nestlings will frequently grow more slowly, fledge at a smaller size, or die from starvation or aggression from older nestlings (Mock and Parker 1998). Siblicide can be facultative or obligate. When siblicide is facultative, aggression and siblicide within a brood may be less frequent when food availability and weather conditions are favourable (e.g. Bortolotti et al., 1989; Reynolds 1996). Egg hormones, parental incubation, and parental feeding behaviour might all modulate competition among nestlings (Mock and Parker 1997; Müller and Groothuis 2013). Weather conditions could act as cues for changes in physiology or behaviour that promote or impede competition among nestlings. If climate change generally results in weather conditions that are unfavourable for growth (less food, increased thermal stress), the strongest impacts of changing weather conditions will likely be on later hatching nestlings.

## 2.6 Weather and the evolution of avian growth

Because weather can influence avian growth in many ways, a change in weather will likely result in altered selection on nestling growth traits and influence the evolution of nestling growth traits that are heritable. To predict the evolution of avian growth traits, we need to understand the evolvability of these traits as well as natural selection acting on them. Both these components of evolution, *i.e.* growth evolvability and natural selection on growth, can change according to environmental variations.

### 2.6.1 Estimation of the evolutionary potential of growth is challenging

Little is known about the heritability of nestling growth traits under different weather conditions, making it difficult to predict how and whether nestling traits will evolve in response to changing climate. Similarly, little is known about how variation in weather affects natural selection on growth traits.

Few studies investigate the heritability of growth parameters such as the asymptote, growth rate, and timing of maximum growth (Fig 2.1) in the wild. In some studies, tarsus length at 13-15 days of age in European starlings is heritable when estimated with either offspring-midparent regressions ( $h^2 = 0.43$  [SE = 0.12]) or full-sibling analyses ( $h^2 = 0.30$  [SE = 0.22]) in a partial cross-fostering experiment (Smith and Wettermark, 1995). Such heritabilities for tarsus length is similar to estimates of heritability of morphological traits in many other avian quantitative genetic studies (Postma 2014). However, when Smith and Wettermark (1995) use an analysis of variance to estimate the heritability of logistic growth curve components fit to the starling's body masses, they find the asymptote to be heritable ( $h^2 = 0.25$  [SE = 0.21]) but not the inflection point or growth constant. Age-specific size and mass measurements are also heritable in great tits ( $h^2$  of fledging mass = 0.24 [SE = 0.02]; Garant et al., 2004).

Advances in statistical techniques used in quantitative genetics now allow a more accurate measurement of the evolutionary parameters of nestling growth in wild populations. Mixed models called ‘animal models’ that use between-individual relatedness within a population and can handle uneven sampling designs offer an improvement over offspring-midparent regressions (Kruuk, 2004; Wilson et al., 2010). Use of an animal model in house sparrows shows the nestling age-specific masses and tarsus lengths to be heritable ( $h^2$  for mass at 5 days = 0.57 [SE = 0.19], mass at 10 days = 0.86 [SE = 0.13]; tarsus at 5 days = 0.81 [SE = 0.22], tarsus at 10 days = 0.63 [SE = 0.11]; Bonneaud et al., 2009). In a more recent large cross-fostering experiment of blue tits, age-specific masses throughout a nestling’s growth period are found to have low heritabilities using an animal model ( $h^2$  ranged from 0.07 [SE = 0.04] at 0 days to 0.09 (SE = 0.03) at 6 days (Hadfield et al., 2013). The authors attributed the low additive genetic variances and heritabilities of nestling age-specific masses to their multivariate statistics and experimental design, where they control for the effects of viability selection when estimating (co)variances among nestlings (Hadfield et al., 2013). Analyses accounting for missing data from individuals that do not survive until nestling mass measurement can help avoid biases in estimates of selection and additive genetic variances for nestling traits (see Hadfield, 2008 for a thorough discussion)

In poultry, growth parameters (asymptote, the timing of maximum growth, growth rate, age-specific mass/size) can be moderately heritable (*e.g.*,  $h^2$  range = 0.15 – 0.66; Grossman and Bohren, 1985; Mignon-Grasteau, 1999; N’Dri et al., 2006; Dana et al., 2011; Haunshi et al., 2012) and selection on domestic species provides evidence that growth traits can evolve under these controlled settings (Marks 1990 as cited in Noordwijk and Marks 1998; Steigner et al., 1992; Zuidhof et al., 2014). Heritability of avian growth might be higher in husbandry settings

compared to wild populations because of controlled rearing conditions, which reduce the amount of environmental variation. Quantitative genetic studies on avian growth in wild conditions are presently too scarce to make more robust conclusions on the expected levels of heritability, so we encourage more studies to estimate the additive genetic variance of nestling growth parameters in wild avian populations.

### **2.6.2 Heritability is environmentally dependent**

An important note relevant to weather conditions is that heritability measures are only applicable to the population and the environment where they are measured. The denominator in the calculation of heritability, phenotypic variance, is equal to the sum of genetic variance and environmental variance. Hence, an increase in the environmental variance of a trait results in a decrease in the heritability estimate. Additionally, environmental variation can impact the level of additive genetic variation estimated for a given trait (Gebhardt-Henrich and Noordwijk, 1994; Charmantier and Garant, 2005; Wood and Brodie, 2016). Early papers measuring the heritability of growth traits noted that poor environmental conditions during growth might restrict the expression of additive genetic variance, resulting in lower heritability of the fledgling or adult phenotypic traits in unfavourable environments (Gebhardt-Henrich and Noordwijk, 1991, 1994; Gebhardt-Henrich, 1992). The original hypothesis of environmental influence on the heritability of growth by Noordwijk (1982 as cited in Noordwijk and Marks 1998) suggests that under unfavourable conditions, a nestling might not reach its genetically determined size, but instead would be constrained because of maturation at a set age. However, under favourable conditions a nestling will reach a final size before age-induced maturation. Therefore, the hypothesis suggests that variation in the asymptote under unfavourable conditions might be more likely to reflect environmental differences among nestlings and the variation under favourable conditions might

reflect genetic differences among individuals (Noordwijk and Marks 1998). A change in the genes that underlie the phenotypic expression of a trait could also cause a change in additive genetic variation between environments (Wood and Brodie, 2016). For example, in a hot environment, genes that play a role in heat tolerance might largely determine the additive genetic variance in a growth trait, while in a thermoneutral environment, genes that play a role in metabolism and growth might explain most of the differences among individual growth trajectories. Therefore, weather variation could affect rates of evolution through an increase or decrease in heritability by increasing or decreasing the environmental and/or the additive genetic contribution to variation in nestling growth traits. Lastly, because heritability is dependent on environmental variance, directly reporting the additive genetic variance of a trait scaled by the mean of the trait will allow accurate comparisons of evolvability across traits and species (Houle, 1992; Hansen et al., 2011). It is important for researchers to report both metrics when trying to evaluate the general evolvability of any trait.

While we might not know how heritability will change with different weather patterns, we do know that annual changes in the heritability of nestling size traits in response to changes in environmental conditions have been observed. Following a brood size manipulation experiment in great tits, Gebhardt-Henrich and Noordwijk (1991) found that heritability of mass at 15 days of age (near asymptotic mass) might be lower in large broods (average  $h^2 = 0.40$  [SE = 0.54]) than in small broods (average  $h^2 = 0.75$  [SE = 0.36]), but only in years when environmental conditions are unfavourable. Notably, standard errors are large, and results are not statistically significant, but this study is one of the earliest to postulate an effect of environmental conditions on evolutionary parameters in nestling traits. In a comparison of age-specific size measurements following a brood size manipulation in blue tits, Kunz and Ekman (2000) detected

high heritability estimates for age-specific tarsus (age 8 & 10 days), wing (age 6 days), and mass (age 6 & 8 days) measurements in smaller compared to larger broods. While not focused on weather conditions, other more recent studies have noted higher heritability in more favourable environments (Charmantier et al., 2004; Garant et al., 2005).

Experimental studies on poultry provide insight into how weather impacts might influence the evolutionary response of chick growth traits. Marks (1996) examined the response to artificial selection for increased 4-week body mass in restricted versus full nutritional diet lines of Japanese quail (*Coturnix japonica*) and found that the restricted diet line had much lower phenotypic increases (no changes in phenotype for many generations) in 4-week body mass. The quail chick's growth conditions are artificial but could indicate that evolutionary changes in nestling size will be slower in environments where weather conditions reduce food availability, as is expected for climate change in many ecosystems.

Generally, these studies indicate that the heritability of fledging mass increases under favourable conditions, but we should cautiously extrapolate from the current literature because the taxonomic range of current results is restricted, and many studies do not investigate the effects of weather. Further, no studies to our knowledge evaluated the changing heritability of growth rates or the timing of maximum growth in wild populations.

### **2.6.3 Perspectives on adding complexity and interactive effects**

Beyond the genetic variance of a trait, the evolution of a trait also depends on its genetic covariance with other traits (Willham 1972; Arnold et al., 2008; Walsh and Lynch, 2018). The evolution of growth traits may be constrained because of genetic correlations among traits. For example, genes that increase asymptotic mass may decrease the maximum growth rate.

Therefore, weather variation could affect the evolution of growth traits by influencing the genetic

covariance among traits. To date, no study has investigated how weather variation shapes genetic covariances among chick growth traits. Hence it is difficult to determine if genetic constraints or the effect of weather on genetic constraints will have an important role in the evolutionary response of avian growth traits to climate change.

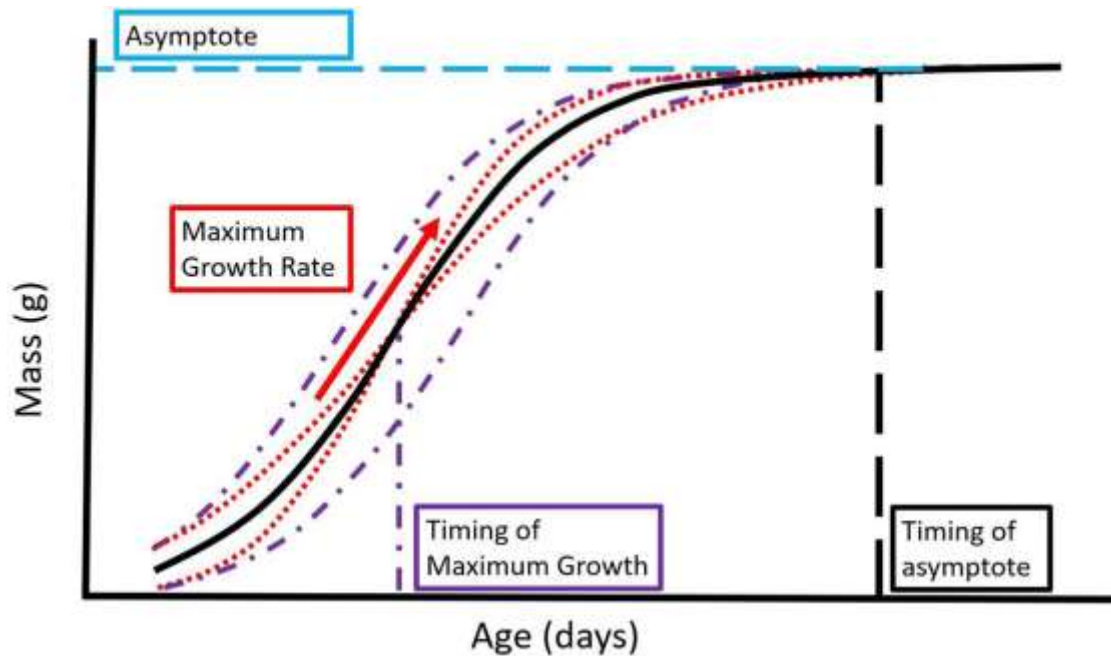
Finally, in addition to a given growth trait's evolutionary trajectory being dependent on genetic correlations, selection on growth traits induced by climate change can interact with other selective forces. For instance, comparative studies have shown that adult and nestling birds are repeatedly smaller in cities than in surrounding rural areas (Bailly et al., 2016; Caizergues et al., 2018). However, as with weather effects, such trends have not yet been attributed to either plastic or evolutionary processes. Several factors that directly influence growth and are affected by climate change (e.g. food availability) are also affected by growing urbanization. Predictive models will hence need at some point to include the complexity of these different and interacting selective forces. Some authors (e.g. Grimm et al., 2008) have hypothesized that since urban areas are 'heat islands,' cities provide an interesting opportunity to study how global warming will impact specific traits (Rivkin et al., 2019). Describing growth curves in urban birds could, hence, be informative in understanding how warmer temperatures and changes in resources influence avian growth. Gene flow from populations adapted to urban habitats into populations in more natural habitats could also provide individuals pre-adapted to warmer conditions (e.g. adaptation with gene flow; Tigano and Friesen, 2016).

## **2.7 Conclusions**

Human-induced warming has resulted in average global temperatures increasing by 1°C since the preindustrial period, and temperatures are likely to increase by 1.5°C or more in the next two to three decades (Intergovernmental Panel on Climate Change, 2018). If the impacts of weather on

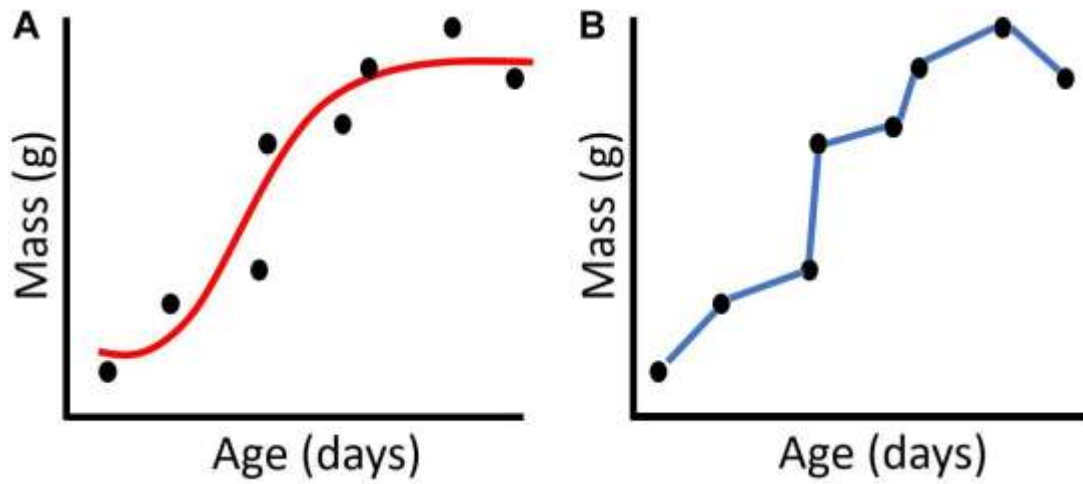
a species are known, qualitative or quantitative predictions for growth trait changes from weather-growth models can be used to predict future growth trait changes. If the additive genetic variance and fitness associated with differences in growth traits can be estimated, these models could be improved with evolutionary and demographic information (Jenouvrier and Visser 2011; Vedder et al., 2013).

We have outlined multiple weather components that affect growth traits of avian species. The future of this research will involve trying to predict adaptive responses to these changes. We think the main questions to address next are: 1) what growth trajectories are adaptive in an environment altered by climate change? 2) what is the potential for a given population of birds to adapt to climate change through either plastic or evolutionary adjustments in growth and development? 3) how will environmental changes alter parental effects on growth? and 4) is the potential for adaptation of growth or development altered by the predictability of weather or environmental conditions? To answer these questions, we need more information on individual fitness and growth curves and the genetic (co)variance of chick growth traits.

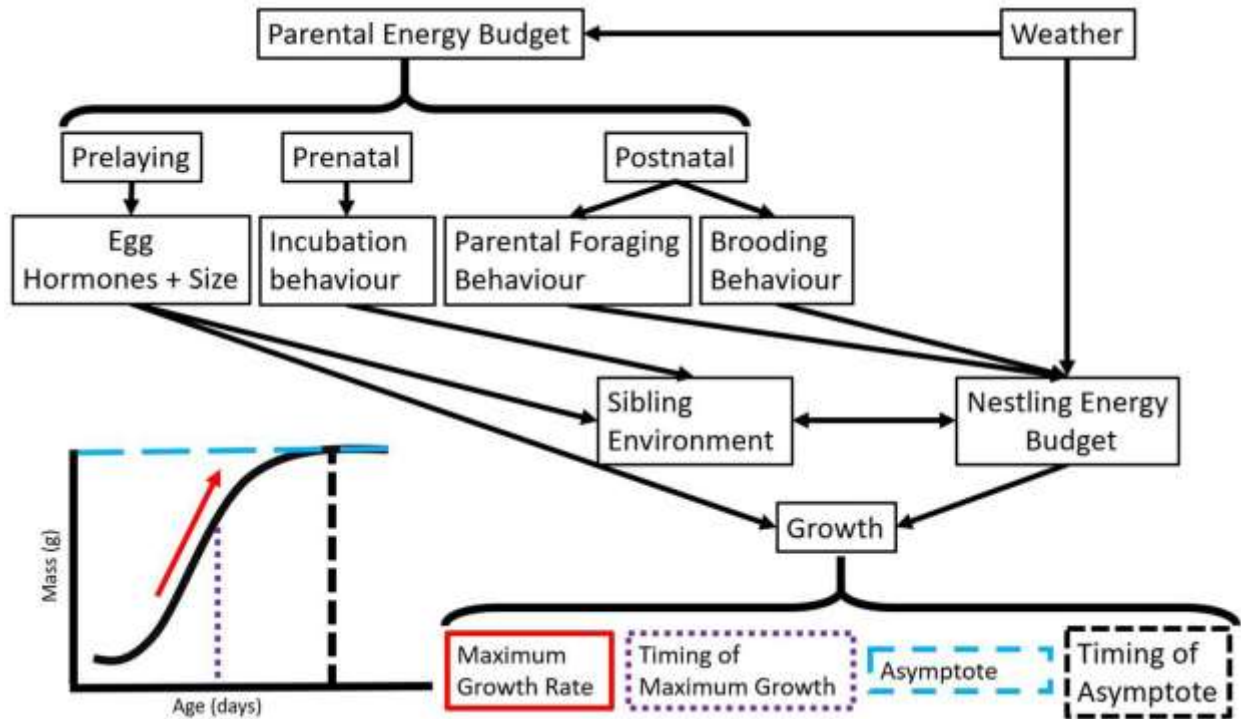


**Figure 2.1: Parameters estimated in a standard logistic curve.**

The maximum growth rate (red arrow) gives an indication of the speed of growth, the asymptote gives an indication of the nestlings' maximum size achieved during the period of study (blue horizontal dash), the timing of maximum growth gives an indication of when during ontogeny maximum growth occurs (purple/vertical dash + dotted line), and the timing of the asymptote might indicate developmental timing (black vertical dashed line). Five growth curves are shown, with the same asymptote but varying in the timing of maximum growth (purple dash and dotted lines) or in maximum growth rate (red dotted lines). All curves have the same asymptote as the reference curve (thick black curve) but vary in their trajectory. If a study of nestling growth only measures mass at the asymptote as in this example, variation throughout the trajectory of the growth curve is hidden. Whether this variation impacts fitness is currently unknown.



**Figure 2.2:** Hypothetical example of a A) function-valued trait approach and a B) character-state approach for modelling a chick growth curve.



**Figure 2.3: Paths by which weather can impact variation in growth as described by parameters estimated from a general logistic curve.**

While we display physical growth in this figure, it will be useful to map the development of tissue functions (e.g. cognition, thermoregulation, motor function) onto this growth curve to compare and contrast development and physical growth over the nestling period. Many of the factors that impact growth are also likely to impact development.

**Table 2.1: Associations between aspects of temperature and nestling growth traits identified from our literature search.**

Temperature variables are sorted in the order maximum, mean, and minimum temperature and alphabetically by first author. Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (-) or not significant (0), and the study reference.

Species	Temperature variable	Association with growth	Study
Zebra Finch <i>Taeniopygia guttata</i>	Mean daily maximum during growth	Mean mass (-) and tarsus length (0)	Andrew et al. 2017
European bee-eater <i>Merops apiaster</i>	Mean daily maximum between hatching and measurements	Residual mass (0)	Arbeiter et al. 2016
Lesser kestrel <i>Falco naumanni</i>	Maximum during 2-day period before measurement	Mass gain in adobe cavity nests (-) Mass gain in wooden nest boxes (-)	Catry et al. 2015
European roller <i>Coracias garrulus</i>	Maximum during 2-day period before measurement	Mass gain in adobe cavity nests (0) Mass gain in wooden nest boxes (-)	Catry et al. 2015
Common fiscal <i>Lanius collaris</i>	Daily maximum	Diurnal change in mass at 6 days of age (-)	Cunningham et al., 2013
Cliff Swallow <i>Petrochelidon pyrrhonota</i>	Mean daily maximum during growth	Nestling mass at age 10 days (-)	Imlay et al. 2018
Lance-tailed manakin <i>Chiroxiphia lanceolata</i>	Mean daily maximum during breeding season	Linear growth rate (-)	Jones and DuVal 2019
Superb Fairy wren <i>Malurus cyaneus</i>	Mean maximum before growth	Mass at age 14 days (+, - quadratic)	Kruuk et al. 2015
Superb Fairy wren <i>Malurus cyaneus</i>	Mean maximum during period the end of the previous breeding season	Mass at age 14 days (-)	Kruuk et al. 2015
Lapland longspur <i>Calcarius lapponicus</i>	Mean maximum during growth	Daily growth rate (+)	Pérez et al. 2016
Pied flycatcher <i>Ficedula hypoleuca</i>	Mean and maximum between mass measurements	Age-specific mass at age 7, 10, & 13 days (+)	Siikamäki 1996
Great tit <i>Parus major</i>	Mean daily during growth	Residual wing length (+)	Eeva et al. 2020
Pied flycatcher <i>Ficedula hypoleuca</i>	Mean daily during growth	Residual wing length (+, - quadratic)	Eeva et al. 2020
Pied flycatcher <i>Ficedula hypoleuca</i>	Mean during growth	Subarctic population residual mass (+) Temperate population residual mass (+)	Eeva et al. 2002
Wryneck <i>Jynx torquilla</i>	Mean hourly during the daytime between measurements	Daily growth of mass and 8 <sup>th</sup> primary from age 14 to 16 days (-)	Geiser et al. 2008

White stork <i>Ciconia ciconia</i>	Mean daily during 7 days of growth	Relative growth rate (+)	Kosicki and Indykiewicz 2011
Adelaide Rosella <i>Platycercus elegans adalaidae</i>	Mean day and night during growth	Nestling linear growth in mass and bill surface area (+)	Larson et al. 2018
	Night-time standard deviation	Nestling linear growth in mass (-)	
Blue tit <i>Cyanistes caeruleus</i>	Mean during 2-day period before measurement	Average 2-day increase in mass (-), head-bill length (-), tarsus length (-), fourth primary length (-)	Mainwaring and Hartley. 2016
Spotless starling <i>Sturnus unicolor</i>	Mean during growth of nestling from first brood	Wing length (+) and bill length (+) at 14 days	Salaberria et al. 2014
	Mean during growth of nestling from second brood	Mass (-), tarsus length (-), wing length (-), and bill length (-) at age 14 days	
Curlew sandpiper <i>Calidris ferruginea*</i>	Mean between growth measurements	Observed/expected growth of mass (+) Observed/expected growth of bill length (+)	Schekkerman et al. 1998
Chaffinch <i>Fingilla coelebs</i>	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Linnet <i>Carduelis cannabina</i>	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Skylark <i>Alauda arvensis</i>	Mean daily minimum during linear growth	Linear mass (+, - quadratic) and tarsus (+, - quadratic) growth rate	Bradbury et al. 2003
Yellowhammer <i>Emberiza citrinella</i>	Mean daily minimum during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Tengmalm's owl <i>Aegolius fenereus</i>	Mean daily during the breeding season	Nestling duration (0)	Kouba et al. 2015
Golden plover* <i>Pluvialis apricaria</i>	Mean daily minimum 2 days prior to measurement	Residual mass (0)	Machín et al. 2018
	Mean daily minimum over age interval	Residual change in mass (+)	

\*Precocial species

**Table 2.2 Associations between aspects of precipitation and nestling growth traits identified from our literature search.**

Precipitation variables are sorted in the order of cumulative, mean, and number of days with, precipitation and alphabetically by first author. Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), or negative (-) or not significant (0), and the study reference.

Species	Precipitation variable	Association with growth	Study
Canada goose <i>Branta canadensis</i>	Cumulative before and after hatch (June/July)	Principle Component 1 of Gosling Size (+)	Brook et al. 2015
Grasshopper Buzzard <i>Butastur rufipennis</i>	Cumulative post-hatch (June/July)	Days to grow from 10% to 90% of final mass (-) Grams per day mass gain from 0 – 10 days (+)	Buij et al. 2013
Tree Swallow <i>Tachycineta bicolor</i>	Cumulative 3 days prior to measurement	Residual mass (-)	Cox et al. 2019
Eurasian bittern <i>Botaurus stellaris</i>	Cumulative between measurements	Daily increase in mass (-) and tarsus length (-)	Kasprzykowski et al. 2014
Pied flycatcher <i>Ficedula hypoleuca</i>	Cumulative between mass measurements	Age-specific masses at age 7, 10, & 13 days (-)	Siikamäki 1996
European bee-eater <i>Merops apiaster</i>	Mean daily between hatching and measurement	Residual mass (0)	Arbeiter et al. 2016
Chaffinch <i>Fingilla coelebs</i>	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Linnet <i>Carduelis cannabina</i>	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Skylark <i>Alauda arvensis</i>	Mean daily during linear growth	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Yellowhammer <i>Emberiza citrinella</i>	Mean daily during linear growth	Linear mass (-) and tarsus growth rate (-)	Bradbury et al. 2003
Wryneck <i>Jynx torquilla</i>	Mean hourly during the day between measurements	Daily growth of mass from age 3 to 5 and 5 to 7 days (-)	Geiser et al. 2008
Blue tit <i>Cyanistes caeruleus</i>	Mean daily 5 days prior to measurement	Nestling mass at 11 days of age (+)	Grzędzicka 2018
White stork <i>Ciconia ciconia</i>	Mean daily during 7 days of growth	Relative growth rate (-)	Kosicki and Indykiewicz 2011
Tengmalm's owl <i>Aegolius fenereus</i>	Mean daily during the breeding season	Nestling duration (0)	Kouba et al. 2015
Fairy wren <i>Malurus cyaneus</i>	Mean before nestling growth	Mass at age 14 days (+)	Kruuk et al. 2015
Blue tit <i>Cyanistes caeruleus</i>	Mean during 2-day period before measurement	Average 2 day increase in mass (+), head-bill length (0), tarsus length (+), & fourth primary length (+)	Mainwaring and Hartley 2016
Lapland longspur <i>Calcarius lapponicus</i>	Mean daily during growth	Daily growth rate (-)	Pérez et al. 2016
Gambel's white crowned sparrow	Mean daily during growth	Daily growth rate (-)	Pérez et al. 2016

<i>Zonotrichia leucophrys gambelii</i>			
Pied flycatcher <i>Ficedula hypoleuca</i>	Mean daily during growth	Subarctic population residual mass (0) Temperate population residual mass (0)	Eeva et al. 2002
Great tit <i>Parus major</i>	Maximum number of consecutive rainy days during growth	Residual wing length (+)	Eeva et al. 2020
Pied flycatcher <i>Ficedula hypoleuca</i>	Maximum number of consecutive rainy days during growth	Residual wing length (+)	Eeva et al. 2020

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**Table 2.3 Associations between combined weather effects, wind speed, sunshine, and nestling growth traits identified from our initial literature search.**

Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (-), or not significant (0), and the study reference.

Species	Weather variable	Association with growth	Study
Blue tit <i>Cyanistes caeruleus</i>	Mean wind speed during 2-day period before measurement	Average 2 day increase in mass (0), head-bill length (0), tarsus length (-) and fourth primary length (+)	Mainwaring and Hartley 2016
Eurasian bittern <i>Botaurus stellaris</i>	Mean wind speed between measurements	Daily increase in mass (-) and tarsus length (-)	Kasprzykowski et al. 2014
Tengmalm's owl <i>Aegolius fenereus</i>	Mean daily wind speed during breeding season	Nestling duration (0)	Kouba et al. 2015
European bee-eater <i>Merops apiaster</i>	Mean daily windspeed between hatching and measurement	Residual mass (0)	Arbeiter et al. 2016
	Mean daily sunshine between hatching and measurement	Residual mass (+)	Arbeiter et al. 2016
Chaffinch <i>Fingilla coelebs</i>	Mean daily sunshine hours during linear	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Linnet <i>Carduelis cannabina</i>	Mean daily sunshine hours during linear	Linear mass (0) and tarsus (0) growth rate	Bradbury et al. 2003
Skylark <i>Alauda arvensis</i>	Mean daily sunshine hours during linear growth	Linear mass (0) and tarsus (-) growth rate	Bradbury et al. 2003
Yellowhammer <i>Emberiza citrinella</i>	Mean daily sunshine hours during linear	Linear mass (0) and tarsus growth rate (0)	Bradbury et al. 2003
Barn Swallow <i>Hirundo rustica</i>	Temperature on day of nestling measurement	Nestling mass at 8-12 days of age (-) - High wind speed dampened effect - High rainfall increased effect	Facey et al. 2020
	Mean temperature between hatching and measurement	Nestling mass at 8-12 days of age (-) - High wind speed dampened effect	
American kestrel <i>Falco sparverius</i>	Principle Component 1 of weather during nestling growth period (associated with increased wind, rainfall, and cold air temperature)	Nestling mass (-) and length of tenth primary (-) at age 20.5 to 24 days	Dawson and Bortolotti 2000

**Table 2.4 Associations between experimental manipulations of environmental conditions and nestling growth traits.**

Columns indicate the species, the weather variable found to be associated with a growth trait, the growth trait and whether the association was positive (+), negative (-), or not significant (0), and the study reference.

Species	Experimental manipulation	Association with growth	Study
Blue Tit <i>Cyanistes caeruleus</i>	Heating of nest during growth	Increase in mass with age (-) Tarsus and wing length at 14 days (0)	Andreasson et al. 2018
Zebra Finch <i>Taeniopygia guttata</i>		Mass and tarsus length at age 28 days (-)	Andrew et al. 2017
Tree Swallow <i>Tachycineta bicolor</i>		Growth rate constant of mass (+), length of ninth primary feather (+), and length of tarsus (0)	Dawson et al. 2005
Great Tit <i>Parus Major</i>		Mass at age 15 days (-)	Rodríguez and Barba 2016b
Great Tit <i>Parus Major</i>	Cooling of nest during growth	Mass at age 15 days (0) Tarsus length at age 15 days (-)	Rodríguez and Barba 2016a
Great Tit <i>Parus Major</i>	Heating of nest during incubation	Age-specific tarsus length, & body mass (0) Mass and tarsus length growth rate (0)	Álvarez & Barba 2014
Carolina Wrens <i>Thryothorus ludovicianus</i>		Nestling period (-) Mass at 9 days of age (-)	Mueller et al. 2019
European starlings	Heating of nest during incubation	Nestling period (0) Mass at 3 days of age (0) Ratio of mass to tarsus cubed at 10 days of age (0)	Reid et al. 2000
Prothonotary warbler <i>Protonotaria citrea</i>		Nestling period (-) Mass at 8 days of age (+)	Mueller et al. 2019
Tree Swallows <i>Tachycineta bicolor</i>		Variation in mass at 1 day of age (-)	Ardia et al. 2009
	Heating at origin nest during incubation	Residual Body Mass at 4 and 7 days of age (+)	Pérez et al. 2008
	Heating at nest of rearing during incubation	Residual Body Mass at age 10 and 13 days of age (+)	
	Decreased nest temperatures during incubation	Residual body mass (-)	Ardia et al. 2010

Blue tits <i>Cyanistes caeruleus</i>		Growth rate (-) Mass at 14 days of age (-)	Nilsson et al. 2008
Mountain blackeye <i>Chlorocharis emiliae</i>	Warming of nest and rain protection during incubation and growth	Nestling period (-), mass growth rate constant (+), wing length growth rate constant (+), tarsus length growth rate constant (+)	Mitchell et al. 2020
Tree Swallow <i>Tachycineta bicolor</i>	Experimental trimming of female ventral feathers	Nestling asymptotic mass (+)	Tapper et al. 2020
Blue tits <i>Cyanistes caeruleus</i>	Experimental trimming of parent's ventral feathers (Control and experimental broods were both enlarged)	Mass of nestlings at 14-days of age (+) - Only for first time breeding females Wing length (+) and tarsus length (0) at 14 days of age	Nord and Nilsson 2019
	Experimental trimming of parent's ventral feathers (Control and experimental broods were both enlarged)	Body mass (0), tarsus length (0), and wing length (0) at 14 days of age	Andreasson et al. 2020

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## Chapter 3

# Environmental conditions variably affect growth across the breeding season in a subarctic seabird

### 3.1 Abstract

Predicting the impacts of changing environments on phenotypes in wild populations remains a challenge. Growth, a trait that frequently influences fitness, is difficult to study as it is influenced by many environmental variables. To address this, we used a sliding window approach to determine the time-windows when sea-surface and air temperatures have the potential to affect growth of black-legged kittiwakes (*Rissa tridactyla*) on a colony in the Northeast Pacific. We examined environmental drivers influencing nestling growth using data from a long-term (21-year) study that food supplements a portion of the colony. The associations between kittiwake growth and climatic conditions in our study indicated that warmer environmental conditions can both positively and negatively impact nestling growth parameters depending on hatching order. We found that first-hatched nestlings had a heavier maximum mass under warm air temperatures and cold sea conditions. Warmer air temperatures negatively affected the second-hatched nestling in a brood. However, when air temperatures were warm, warmer sea-surface temperatures predicted heavy, fast-growing second-hatched nestlings in contrast to what we observed for first-hatched nestlings. Food supplementation alleviated the temperature effects, and competition among nestlings influenced how strongly a variable affected growth. We identified windows that might indicate specific biological pathways through which environmental variation affected growth directly or indirectly. Overall, our windows suggest that nestlings in shared nests will be most affected by warming conditions.

### 3.2 Introduction

Ongoing global changes are affecting the thermal environment and resource availability for many species across the globe (Intergovernmental Panel on Climate Change, 2018). One important consequence of these abiotic changes is the altered development and growth of offspring. Environmental conditions during early-life can affect an organism's phenotype and fitness (Bateson 1979; Cooper and Kruuk 2018; English et al. 2016; Lindström 1999; Metcalfe and Monaghan 2001). For example, early-life growth traits often predict adult size (Huchard et al. 2014; van Gils et al. 2016), a trait that is frequently under directional selection (Kingsolver and Diamond, 2011). How global environmental change affects fitness may depend on the contribution of the early-life environment to growth, and early-life traits to adult fitness.

Studying growth is complex because growth can be affected directly and/or indirectly by a multitude of environmental variables with cumulative effects. Environmental conditions might directly affect the thermal environment that a juvenile experiences during growth or indirectly affect growth by changing parental care or food availability (e.g. Andreasson et al. 2018; Kruuk et al. 2015; McAdam and Boutin 2003; Rollinson and Rowe 2015). Despite these difficulties, globally changing conditions seem likely to affect growth for many species, making it essential to quantify the impact of new environments on growth (Noble et al. 2018; Sauve et al. 2021).

Whereas resources drive organismal growth, temperature determines the efficiency of metabolic processes (Angilletta 2009). As such, temperature extremes may impact the rate of growth and development of tissues. While endothermic animals can regulate their body temperature, thermoregulation often involves trade-offs in energy allocation (Dmitriew 2011). To reduce the energy expenditure of thermoregulation and limit the impacts of unfavourable temperatures, some species may anticipate stressful conditions and either slow development to wait for suitable conditions, or accelerate development to reach maturity earlier at a smaller size

(Brannelly et al. 2019; Emlen et al. 1991). However, because of genetic, environmental or parental differences, individuals might differ in their ability to adjust their growth to their ambient temperature (e.g. Angilletta 2009 pg.159; Vega-Trejo et al. 2018). For many animal species, such inter-individual variation will be challenging to measure, but in theory, different growth responses could play an important role in adaptive or maladaptive responses to novel environmental conditions (Chevin et al. 2013).

In this study, we estimated the effects of two environmental variables (sea-surface and air temperature) on multiple components of nestling growth in a wild population of black-legged kittiwakes (*Rissa tridactyla*). The colony of black-legged kittiwakes on Middleton Island, Alaska, has been studied for over two decades as an indicator of ecosystem function in the Gulf of Alaska and Prince William Sound. On Middleton Island, researchers experimentally supplement a portion of the population of kittiwakes with food (hereafter “fed”; versus non-food-supplemented “unfed”; Gill and Hatch, 2002). We used data on nestling growth, combined with experimental and natural variation in environmental conditions, to investigate weather influences on nestling growth curves of black-legged kittiwakes. Specifically, we investigated 1) if climate and nestling growth traits changed over 21 years of study, 2) during which time-window across the nestling period (i.e. before fledging) do air and sea-surface temperatures affect nestling growth (Table 3.1; H1), 3) whether air temperature and food conditions (sea-surface temperature and experimental food supplementation, see below) individually and interactively affect the growth phenotype of a nestling (Table 3.1; H2.1, H2.2, and H2.3), and 4) whether the effects of environmental conditions differ for older and younger siblings in a brood (Table 3.1; H3).

We framed our hypotheses around three parameters of a nestling growth curve (Appendix A Fig. A1; Table 3.1): the asymptote (maximum weight), the timing of maximum growth

(inflection point), and the maximum relative growth rate (growth rate; Tjørve and Tjørve 2017). We expected the timing of maximum growth and growth rate to be influenced by environmental windows earlier in the breeding season than the asymptote (H1) because the maternal environment during prelaying may influence egg size and early growth (Williams 2012). We expected cold sea-surface temperatures to be associated with large, fast-growing nestlings because these conditions correlate with high reproductive success for Middleton's kittiwakes due to increases in capelin *Mallotus villosus* abundance (H2.1; Hatch 2013). In years with warmer sea-surface temperatures, there is a notable reduction in the proportion of capelin in the kittiwake diet and kittiwakes tend to forage on a higher proportion of herring *Clupea pallasii*, invertebrates (e.g. Euphausiidae, Copepoda, Cephalopoda: Gonatidae), myctophids Myctophidae, sablefish *Anopoploma fimbria*, salmon *Oncorhynchus* spp. and sand lance *Ammodytes hexapterus* (Hatch 2013). We assumed that small and slow-growing nestlings were indicators of a stressful thermal or resource environment. We expected that warmer air temperatures would be associated with improved growth because current air temperature conditions are below the thermal neutral zone of nestling kittiwakes (H2.2; Bech et al. 1984). Nestlings become homeothermic at 6-8 days of age so warmer temperatures might improve growth directly by providing a better thermal environment or indirectly by allowing parents to spend less time brooding and more time foraging (Hatch et al. 2020). We predicted that fed nestlings would be less affected by air temperatures because they might have had more energy available for thermal regulation and growth (H2.3). Finally, because black-legged kittiwakes exhibit facultative siblicide, we expected the growth of first-hatched nestlings to depend on how long a first-hatched nestling shared a nest with a second-hatched nestling (Merkling et al. 2016; H3).

### **3.3 Materials and methods**

#### **3.3.1 Black-legged kittiwake colony and environmental variation**

We used 21 years (1998-2018) of data from a colony of black-legged kittiwakes on Middleton Island (59°26'N, 146°20'W) in the Gulf of Alaska (Gill and Hatch 2002). On Middleton Island, black legged-kittiwakes nest in an abandoned radar tower. The tower is a 12-walled polygon where artificial nest sites have been created on the upper walls, allowing observations through one-way glass windows from inside the tower. Each year, research teams provide a subset of the nesting pairs with capelin through a PVC tube at their nest site three times a day from May until mid-August (further details in Gill and Hatch 2002). The same group of nesting sites are designated as food supplemented sites each year but parental pairs at fed sites will change because of death or competition for sites.

Nests are checked twice daily (9:00 and 18:00 H) throughout the season to record laying and hatching. Once hatched, nestlings are weighed every 5 days from hatching to 40 days (i.e. close to fledging). Within a brood, eggs hatch asynchronously with an average difference of 1.64 days between the first and second laid egg (Merkling et al. 2014). In each year of the study, the first hatched (“alpha”) and second hatched (“beta”) nestlings are marked with a nontoxic colour marker to distinguish nestling rank. Mass is weighed to the nearest 0.1 g using an electronic scale. Several experiments have been conducted on the nests in the past (e.g. Merkling et al. 2014, 2016), so we excluded data from any nestlings that have been experimentally manipulated (~9.1% of breeding attempts excluded, beyond food supplementation).

#### **3.3.2 Predictor variables**

We evaluated sea-surface temperature and air temperature as environmental variables that potentially influence nestling growth. Air temperature data were collected from the Middleton

Island airport weather station (~2 km from the kittiwake radar tower; <https://www.ncdc.noaa.gov/cdo-web/cart>). Version 2 of the advanced very high-resolution radio meter dataset (AVHRR) daily sea-surface temperature data was collected from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC; <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.OISST/.version2/.AVHRR/.sst/>). All pixels within a 100 km radius of Middleton Island were averaged each day for sea-surface temperatures within the region.

### 3.3.3 Statistical analyses

#### 3.3.3.1 Baseline models

Because we hypothesized that weather affected nestling growth differently depending on hatch order and treatments (fed versus unfed; H2.3 and H3), we ran four non-linear mixed models for each nestling rank and food supplementation treatment (Alpha-Unfed, Beta-Unfed, Alpha-Fed, and Beta-Fed). We used Bayesian non-linear multi-level models to model nestling growth with a unified Richard's curve fit to nestling data using the R package 'brms' (Bürkner 2017). The unified Richard's curve is a reparameterization of the Richard's curve, which is a generalized version of a logistic curve (Sugden et al. 1981; Tjørve and Tjørve 2017) (Model 1):

$$W = A \left( 1 + (d - 1) \cdot \exp \left( \frac{-k(t - T)}{d^d / (1 - d)} \right) \right)^{1/1-d} + \varepsilon, \quad (1)$$

$$A + k + T \sim 1 + Z_1 I + Z_2 Y,$$

$$d \sim 1$$

where  $A$  is the asymptote or maximum size reached during growth in grams,  $k$  is the maximum relative growth rate (absolute maximum growth rate in grams per day when multiplied by the asymptote),  $d$  affects the shape of the growth curve (sigmoid when greater than 0),  $T$  is the age in days at maximum growth,  $t$  is the age in days of a nestling,  $\varepsilon$  is a vector of the residual effects,  $I$  is a vector of individual effects,  $Y$  is a vector of hatch-year effects, and  $Z_{1-2}$  correspond to identity matrices for individual and year effects respectively. Additionally, we estimated the correlation among all non-linear parameters ( $A$ ,  $k$ ,  $T$ ) at the individual and annual level within the model. We only estimated the shape parameter ( $d$ ) at the population level. To help with convergence, we estimated the asymptote parameter as two orders of magnitude lower and the growth rate parameter as two orders of magnitude higher by multiplying or dividing the parameter within the unified Richards curve, respectively. We used normal priors with a mean of 4.0, 5.0, 15.0, and 2.0, and standard deviations of 1.0, 1.0, 2.0, and 0.5 for the asymptote ( $A$ ), growth rate ( $k$ ), inflection point ( $T$ ), and shape parameter ( $d$ ). We used the default half-Student\_ $t$  distribution priors with a mean of 0, degrees of freedom of 3, and a standard deviation that is equal to the standard deviation of the response variable ( $W$ ; nestling weight) for estimates of the individual ( $I$ ), annual ( $Y$ ) and residual ( $\varepsilon$ ) standard deviation. Details of a similar model we use to evaluate whether there are trends in growth parameters across years are included in Appendix A.

### 3.3.3.2 Hypotheses 1: Timing of environmental predictors of growth

We performed sliding window analyses using the R package ‘climwin’ (van de Pol et al., 2016).

A sliding window analysis identifies a time window for which an environmental variable of interest best explains variation in a measured biological trait. We used relative windows that assume each individual record will be impacted by climate at different times relative to a biological observations' timing. The sliding window analysis varies the start and duration of

windows in increments of days and compares both linear and quadratic relationships between the mean, minimum, and maximum values of climatic variation for a given time window and individual estimates of model parameters. The calculation of individual growth parameters and our sliding-window model comparison are in Appendix A.

To interpret identified windows, we binned them into breeding season categories relative to 40 days after hatching: “Breeding Season” = 120 to 0 days, “Growth” = 40 to 0 days, “Incubation” = 70 to 41 days, & “Prelaying” = 120 to 71 days. Day “0” in these categories is when nestlings would be 40 days of age and day “120” is the beginning of the breeding season. Categories are based on estimates for the nestling, incubation, and follicle development period in kittiwakes (Roudybush et al., 1979). “None” indicated that all sliding windows identified in the sliding window analysis had a probability greater than 0.05 of being detected just by chance.

### 3.3.3.3 Hypotheses 2.1, 2.2, & 2.3: Environmental effects on growth

Once we identified climatic windows using *climwin*, we evaluated them in a model that estimates the statistical effects of each window on all growth curve parameters (Model 2):

$$W = A \left( 1 + (d - 1) \cdot \exp \left( \frac{-k(t - T)}{d^d / 1 - d} \right) \right)^{1/1-d} + \varepsilon, \quad (2)$$

$$A \sim Xb_A + Z_1I + Z_2Y,$$

$$k \sim Xb_k + Z_1I + Z_2Y,$$

$$T \sim Xb_T + Z_1I + Z_2Y,$$

$$d \sim 1$$

where  $X$  is a matrix of the predictor variables for each parameter (the observed sliding window values specific to each individual), and  $b_A$ ,  $b_k$  and  $b_T$  are vectors of the fixed effects specific to the asymptote, maximum growth rate, and timing of maximum growth (effects of windows of

sea-surface and air temperature identified by the sliding window analysis). We ran models for sea-surface and air temperature separately. Finally, we ran a model where we only retain the fixed effects when the 95% CI of the posterior that did not span zero in sea-surface and air temperature models and combine them into one model. We chose this approach to evaluating our effects in a final model, rather than an information criterion approach, to restrict the combination of window-effects evaluated and keep model choice simple to reduce computation time. This final model included the fixed effects for each parameter and an additional interaction effect between air and sea-surface temperature windows if we retained both an air and sea-surface temperature window for a parameter ( $A$ ,  $k$ ,  $T$ ). Our approach to interpreting interactions is detailed in the Appendix A. Priors for our environmental models were identical to those used in initial growth models above with the addition of a Student-t prior for fixed effect coefficients with a mean of 0, a standard deviation of 5, and 10 degrees of freedom.

#### 3.3.3.4 Hypothesis 3: Interaction of competition and environmental conditions

Alpha nestlings experience different competition environments in that some are the only nestling in the brood, whereas others share the nest with a beta nestling and may have to compete for food and parental care. We included an additional growth model for alpha nestlings from each treatment to determine if competition between nestlings changed the environmental windows detected. Our additional models were identical to the growth models we described above but included a fixed continuous effect of the number of days an alpha nestling overlaps with a beta nestling (range 0-40 days) and the interaction of the number of days and the weather variables in the model.

## **3.4 Results**

### **3.4.1 Models of nestling growth and trends over time**

The dataset included 8198 records of mass from 1190 unfed alpha nestlings ( $\bar{n} = 6.8/\text{nestling}$ ), 3522 records of mass from 788 unfed beta nestlings ( $\bar{n} = 4.4/\text{nestling}$ ), 7415 records of mass from 994 fed alpha nestlings ( $\bar{n} = 7.5/\text{nestling}$ ), and 4089 records of mass from 676 fed beta nestlings ( $\bar{n} = 6.1/\text{nestling}$ ). Growth parameters varied among individuals and years, and the timing of maximum growth and maximum growth rate was correlated in all models (Appendix A Table A1). In more recent years unfed alpha, unfed beta, and fed beta nestlings had on average lighter asymptotes than at the beginning of the study (Appendix A, Tables S2-3, 5). However, there were no linear or quadratic trends over time for the fed alpha nestlings' asymptote (Appendix A Table S4). All nestlings, including fed alpha nestlings, tended to grow more slowly and exhibit maximum growth at an older age in more recent years when compared to nestlings growing in early years of the study (Fig. 3.1; Appendix A Tables S2-5). Increasing overlap with a beta nestling in the nest correlated with a faster maximum growth rate and earlier timing of maximum growth for alpha nestlings (Appendix A Table S6, S7).

### **3.4.2 Annual variation in sea-surface and air temperature during the breeding season**

Average sea-surface and air temperatures varied among years (Appendix A Tables A10, A11; Appendix A Figs. A11, A12). The average sea-surface temperature during the breeding season increased by  $0.43^{\circ}\text{C}$  over the course of the study (95% CI =  $[0.05^{\circ}\text{C}, 0.81^{\circ}\text{C}]$ ; or  $0.02^{\circ}\text{C}$  per year, 95% CI =  $[0.002^{\circ}\text{C}, 0.04^{\circ}\text{C}]$ ) and air temperatures during the breeding season increased by  $0.74^{\circ}\text{C}$  (95% CI =  $[0.32^{\circ}\text{C}, 1.15^{\circ}\text{C}]$ ; or  $0.04^{\circ}\text{C}$  per year, 95% CI =  $[0.02^{\circ}\text{C}, 0.05^{\circ}\text{C}]$ ).

### **3.4.3 Hypotheses 1: Timing of environmental predictors of growth**

For both air and sea-surface temperatures, our sliding window analysis tended to identify climatic windows during the prelaying period as the best predictors of maximum growth rate and timing of maximum growth (Table 3.2). The time window of climatic variation that predicted the asymptote varied but generally included the growth period or encompassed the entire breeding season (Table 3.2; Appendix A Table S8). We identified fewer windows from the sliding window analysis that predicted growth variation for the food-supplemented nestlings (Table 3.2; Appendix A Table S8). Our environmental models of food-supplemented nestling growth only included a window of air temperature during the prelaying period (days) that was a predictor of the timing of maximum growth. Temperatures within each window that we identified with our sliding window analysis increased throughout the study (Appendix A Figs. S3-S8).

#### **3.4.4 Hypotheses 2.1, 2.2, & 2.3: Environmental effects on growth**

Warmer maximum air temperatures and colder minimum sea-surface temperatures throughout the season correlated with heavier asymptotes in unfed alpha nestlings (Fig. 3.2; Appendix A Table A12; Table 3.3). In contrast to alpha nestlings, breeding seasons with a low minimum air temperature tended to result in faster-growing and larger unfed beta nestlings (Fig. 3.3 A, B; Table 3.3; Appendix A Table A13). The average sea-surface temperature of the season had a small effect on the growth of a beta nestling if the season's minimum air temperature was cold. Nestlings that grew in a warm minimum air temperature season and a warm average sea-surface temperature season grew faster and to a larger asymptote than those that grew in a season with warm minimum air temperature and a cold average sea-surface temperature (Fig. 3.3A). Warm minimum sea-surface temperatures during prelaying correlated with slow growth and light asymptotes when the minimum air temperature of a season was low, but fast-growing nestlings when the minimum air temperature of a season was high (Fig 3.3B).

Food-supplemented alpha nestlings that grew in seasons with lower minimum air temperatures during the prelaying and incubation periods exhibited maximum growth at a younger age (Table 3.3; Appendix A Fig. S9). None of the windows that our sliding window analysis identified impacted growth parameters in fed beta nestlings (Table 3.3).

### **3.4.5 Hypothesis 3: Interaction of competition and environmental conditions**

Our sliding window analysis on growth parameters from a model for alpha nestlings that included overlap with beta nestlings showed two main effects. First, the model showed that the average sea-surface and air temperature of the breeding season were predictors of the asymptote of an unfed alpha nestling. Second, the model showed that windows of air and sea-surface temperature during the prelaying period were predictors of the maximum growth rate and the timing of maximum growth rate (Appendix A Table S9).

Controlling for nestling competition revealed some nuance to the effects of temperatures on unfed alpha nestling growth. Increases in days of overlap with a beta nestling resulted in heavy alpha nestlings in seasons with warm average air temperatures, but light alpha nestlings in seasons with warmer average sea-surface temperatures (Fig. 3.2). Overlap models demonstrated that warmer average air temperature and colder minimum air temperatures during prelaying resulted in fed alpha nestlings that exhibited maximum growth at a younger age, but this effect was weaker the more days an alpha nestling overlapped with a beta (Appendix A Fig. A10 A, B). Further, controlling for overlap with a beta nestling in food supplemented alpha nestlings revealed an association of a warmer average sea-surface temperature with lighter asymptotes in fed alpha nestlings (Appendix A Fig. A10 C).

### 3.5 Discussion

We examined the effects of thermal conditions on kittiwake nestling growth in alpha and beta nestlings, a portion of which were food supplemented to ease dietary constraints. Our results were concordant with carry-over effects from the prelaying period impacting growth rate parameters. In contrast, asymptotic size was largely dependent on weather variation during growth. Avian maternal effects are typically strong right after hatching and subsequently weaken during development (Williams 2012; Williams and Groothuis 2015). Therefore, we expected the prelaying environment to affect traits expressed earlier during growth (maximum growth rate and timing of maximum growth) while we expected environmental effects during the growth period to influence traits expressed later during growth, like the asymptote (Table 1 P1.1 and P1.2). Our sliding window analysis frequently, but not always, identified environmental variation in the prelaying period to best predict the timing of maximum growth and the maximum growth rate, while windows that best predicted the asymptote tended to occur during the growth period or over the entirety of the breeding season (Table 3.2). Weather during the prelaying period might influence food resources available during growth, or carry-over effects might impact parental behaviour during growth. Kruuk et al. (2015) and Marques-Santos and Dingemanse (2020) used a sliding window approach and found that weather conditions during the growth period likely influenced the 14-day masses of nestlings (which might be comparable to our asymptote parameter) in superb fairy-wrens *Malurus cyaneus* and great tits *Parus major*. However, Kruuk et al. (2015) also identified windows before the growth period that influenced 14-day mass. Future studies should investigate when and how environmental conditions affect growth traits in a diversity of species and locations to confirm that early and late breeding season environments most strongly affect traits early and late in ontogeny, respectively.

### **3.5.1 Sea-surface temperature effects on kittiwake nestlings**

Altered sea-surface temperatures can change the phenology, distribution and abundance of prey species for seabirds and decrease the growth of nestlings (e.g. Hedd et al. 2002). Because our windows of sea-surface temperature occur during the nestling growth phase for alpha nestlings, we suspect the smaller asymptotes indicate lower availability of preferred prey species to kittiwakes during the growth period (decreases in proportion of capelin in diet). As warmer sea-surface conditions are related to an increased proportion of less favourable prey sources in the kittiwake diet (herring, invertebrates, myctophids, sablefish, salmon, and sand lance) on Middleton Island (Hatch 2013), we predicted that warmer sea-surface temperatures would correlate with slower growth, smaller asymptotes, and older ages at maximum growth (Table 3.1 P2.1). We observed a slight decrease in alpha nestling asymptotes when sea-surface temperatures are on average warmer during the growth period. In black-legged kittiwakes on Middleton Island warmer years correlate with a decrease in productivity, a decrease in preferred prey (capelin), and an increase in foraging distance of adult birds (Hatch 2013; Osborne et al. 2020). Kittiwakes on Middleton seem to have to search a larger area for profitable foraging areas in warm years but can stay close to the colony in cold years when capelin are available close to the colony (Osborne et al. 2020).

### **3.5.2 Air temperature effects on nestling kittiwakes**

For cold-climate species, warmer air temperatures may be beneficial because they may decrease nestling energy expenditure on thermoregulation and parental energy expenditure on brooding (e.g., McKinnon et al. 2013). We expected that colder air temperatures would slow growth and decrease the asymptotic size (Table 3.1 P2.2). Our results indicated that warmer air temperatures correlated with alpha nestlings that grow to a heavier asymptote (Fig. 3.2; Appendix A Table

A12) yet slower-growing beta nestlings that reach a lighter asymptote (Fig. 3.3A, B; Appendix A Table A13). Because the air temperature windows identified for the alpha and beta nestlings are broad, encompassing most of the breeding season, it is challenging to attribute air temperature variation to a particular breeding stage. Air temperature effects could represent direct effects on nestling growth or indirect effects via parental foraging. In wild bird populations, warmer air temperatures can correlate with fast-growing and heavy nestlings and slow-growing small nestlings (e.g. Andrew et al. 2017; Cunningham et al. 2013; Hiraldo 1990). Nestlings that experience temperatures outside their thermal limit will experience adverse effects, and different temperature changes experienced by populations and variation among species' thermoregulatory ability likely explain contrasts among studies (reviewed in Sauve et al. 2021). Currently, warmer air temperatures appear to improve alpha nestlings' growth and may continue to do so until ambient temperatures exceed the thermal neutral zone for kittiwake nestlings, between 33°C and 35°C for newly hatched nestlings (Bech et al. 1984).

In contrast to patterns found in alpha nestlings, the effect of the minimum air temperature window on beta nestlings did not follow our prediction that warmer minimum air temperatures result in heavy and fast-growing nestlings (P2.2). It seems unlikely that the air temperature effect on beta nestling growth resulted from a direct effect because air temperatures did not exceed the thermal neutral zone of nestling kittiwakes (Bech et al. 1984). However, the negative effect of warming on growth could represent an indirect effect or predictor of food resources, parental care, or egg hormones. Contrasting impacts of warmer air temperature could suggest increased parental investment in the alpha nestling and negative impacts of sibling aggression towards the beta nestling under difficult foraging conditions (Drummond 2001). The amount of parental care provided to the beta nestlings might depend on environmental conditions. In many species,

parents overproduce young and use various brood reduction mechanisms to match local environmental conditions (Braun and Hunt 1983; Mock and Parker, 1997). Food availability or other environmental cues, such as effects of sea-surface temperature on beta nestlings discussed below, could also alter parental care during nestling growth to allow or prevent brood reduction. (e.g. parental compensation, Shizuka and Lyon 2013).

Air temperatures did not appear to affect food-supplemented beta nestlings, but food-supplemented alpha nestlings growing in years with warmer minimum air temperatures during the prelaying/incubation period exhibited maximum growth rate at an older nestling age. We did not expect weather variation to affect food-supplemented nestlings because increased resources are available for thermoregulation and growth (P2.3.1). However, the effect we detect is arguably minor, requiring a large temperature difference to detect a subtle shift in the timing of maximum growth (Appendix A Fig. S9). Controlling for resources experimentally might help reveal some of the small direct effects of temperature on the nestling growth curve. Air temperatures could also be correlated to cues that mothers use as predictors of environmental conditions during the growth period (Giordano et al. 2014; Mousseau and Fox 1998), potentially suggesting that the effect we detected in fed alpha nestlings is an effect of early breeding season environments.

### **3.5.3 Interactive effects of sea-surface and air temperature on nestling kittiwakes**

Because sea-surface temperature is often related to the level of food resources available for seabirds and is related to food conditions for kittiwakes on Middleton (Furness 2016; Hatch 2013), we expected nestling kittiwakes experiencing cold sea-surface temperatures during growth to be less affected by air temperature variation (P2.3.2). The interactions between air and sea-surface temperature do not support this prediction for unfed alpha or beta nestlings. In fact,

warmer air temperatures predict large alpha nestlings, and in unfed beta nestlings warmer sea-surface temperatures are associated with larger, faster-growing nestlings under warm air temperature conditions.

The effect of sea-surface temperature on unfed beta nestlings was dependent on the minimum air temperature of the breeding season. Under cold minimum air temperatures, warmer average sea-surface temperatures during the breeding season had little effect on beta nestlings' growth curve. However, when air temperatures are warm, warmer average sea-surface temperatures during the season resulted in beta nestlings that grew slightly faster to a larger size relative to nestlings that grew in a season with colder average sea-surface temperatures (Fig. 3.3A). An observation of a similar interaction between air and the sea-surface temperatures occurred for minimum sea-surface temperatures during the prelaying period (Fig. 3.3B). Interpreting the consequences of warmer sea-surface temperature on nestling growth is more challenging for beta nestlings than alpha nestlings. Perhaps cues from air or sea-surface temperature during any of these periods are informative for improving nestling growth conditions (Marshall and Uller 2007). Alternatively, better growth of beta nestlings in warmer sea-surface temperature conditions could represent an effect of “high-quality” parents (Coulson and Porter 1985). Parents that successfully raised beta nestlings warm conditions might be parents that are investing extensive effort into all nestlings (Weimerskirch 1992; Winkler 1987).

#### **3.5.4 Competition among siblings**

Competition among siblings might make them more sensitive to environmental effects. Whereas some alpha nestlings compete with a beta nestling throughout most of the growth phase, others (~43%) never compete with a beta sibling because of reduced clutches or early life mortality of beta nestlings. We expected alpha nestlings to be more susceptible to environmental effects the

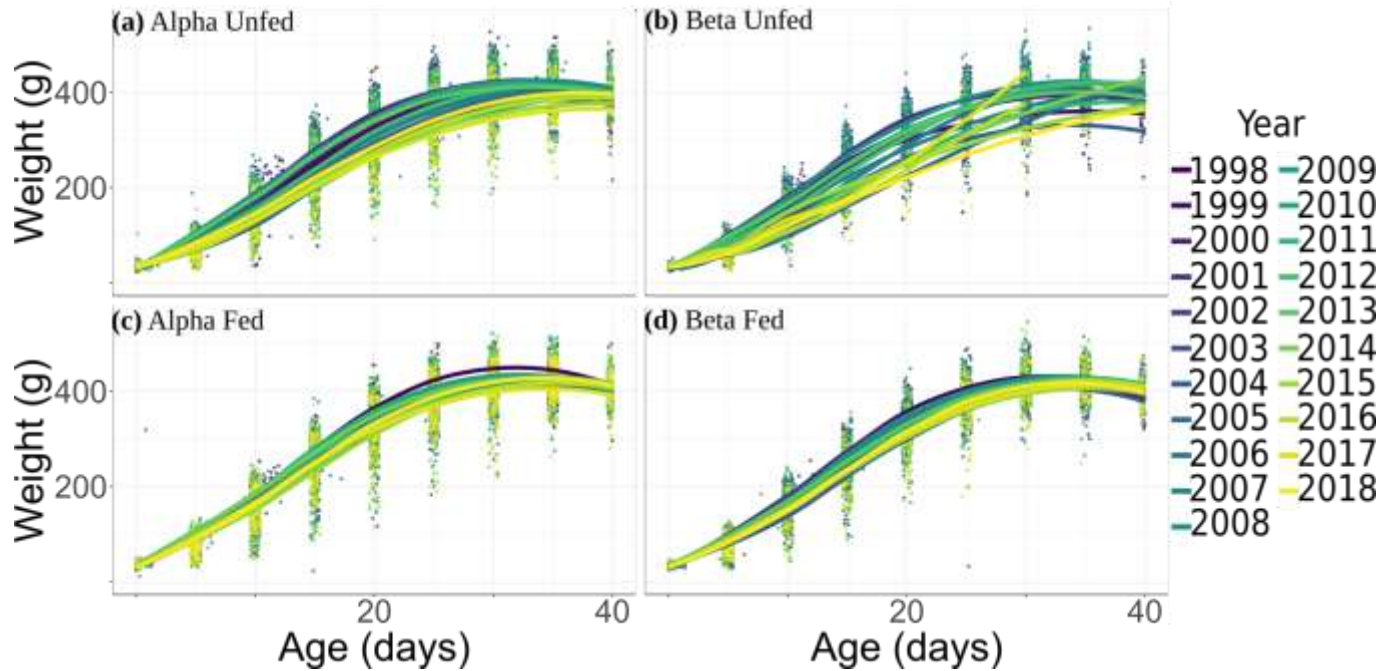
longer they had to share a nest with a sibling (H3). We found that increasing overlap with a beta nestling indeed amplified the positive effects on growth of a warmer air temperature season and the negative effects of warmer sea-surface temperatures (P3; Fig 3.2 A, B). For fed alpha nestlings, more overlap with a beta nestling dampened the overall effects of the average air temperature of a season and the minimum air temperature during the prelaying period on the timing of maximum growth (Appendix A Fig. A10 A, B). Further, when we accounted for sibling competition, our model included a negative effect of warmer sea-surface temperatures on fed alpha nestlings' asymptote (Appendix A Fig. A10 C). Our models of fed alpha nestlings suggest effects that are small and difficult to explain and might be the result of cues used by parents in warm conditions that change alpha nestling growth directly, or the influence of competition with beta nestlings on alpha nestlings.

### **3.5.5 Implications for kittiwakes under climate change and future directions**

Hatching order is likely to affect the sensitivity of growth to environmental conditions (Sauve et al. 2021). Our results suggest that beta kittiwake siblings are likely to be the most strongly affected by a changing climate. Beta kittiwakes are the most strongly affected by weather variation, and warmer conditions tend to result in smaller beta nestlings, suggesting that raising a second nestling is more difficult in warmer conditions. Comparison of the overall fitness of parents caring for beta nestlings, and those without, in future warming scenarios could help determine if investment in beta nestlings is adaptive under warming conditions. Pacific black-legged kittiwakes (*R. t. pollicaris*) are hypothesized to follow a slower life-history strategy than Atlantic black-legged kittiwakes (*R. t. tridactyla*) and limit parental care under stressful conditions to invest in their own survival (Coulson 2002; Schultner et al. 2013). The slower pace of life in Pacific kittiwakes is hypothesized to have evolved because of more variable oceanic

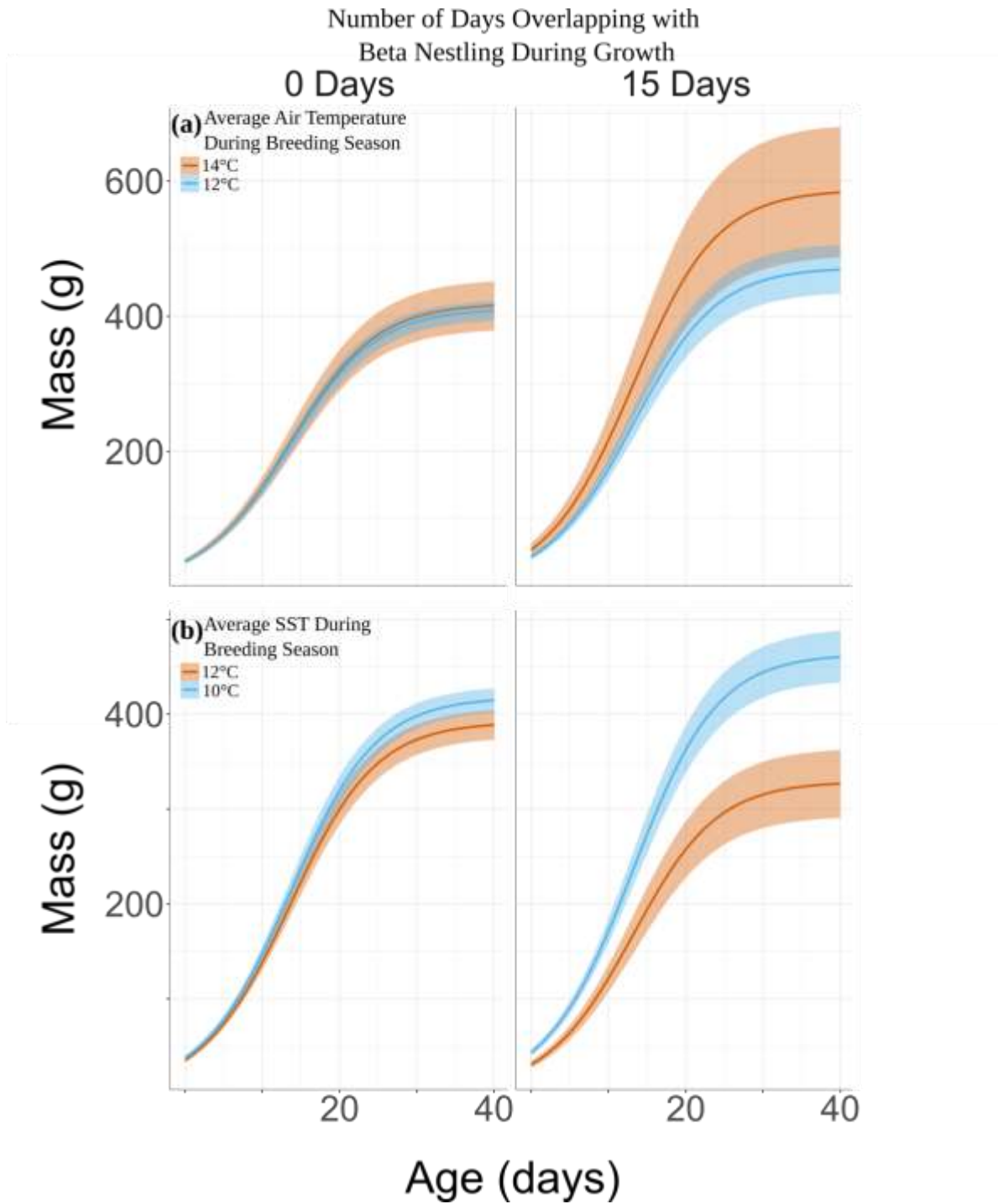
conditions in the Pacific (Suryan et al. 2011). We observe potentially decreased investment in beta nestlings under warmer conditions. Whether this potential decrease in nestlings is adaptive depends in part on how adult survival shifts with warming (Cotto et al. 2019).

Improved understanding of growth in shifting environments will come from continued long-term studies, and the identification of environmentally sensitive windows. Experimental manipulation of growth conditions may help identify the impact of environmental conditions during different periods of the breeding season (Noble et al. 2018; Sauve et al. 2021). We focused on nestlings in this paper, but a large component of nestling traits are determined by the environments that parents experience, suggesting it will be important to understand how environmental variation affects parental care and foraging (Mueller et al., 2019). Further, much of a nestling's growth environment may be linked to the laying and hatching date of their brood, and integrating this information may help describe pathways through which the environmental conditions affect nestling growth (e.g. McKinnon et al. 2012). Once we measure the heritability of growth traits and the natural selection operating on growth curves across different environments, we can aim to predict evolutionary implications of environmental change on nestlings (Sauve et al. 2021). The evolution of growth traits is also likely shaped by predation, which is changing for many species across the globe (Dmitriew 2011; Parmesan 2006). Hence, in addition to the impacts of weather, the selection imposed by changing predation will be important to consider. Ultimately, we show that patterns of kittiwake growth are associated with thermal environments within the breeding season. Associations between air and sea-surface temperature with nestling growth rate and sibling conditions may help predict the potential effects on nestling success under further environmental changes.



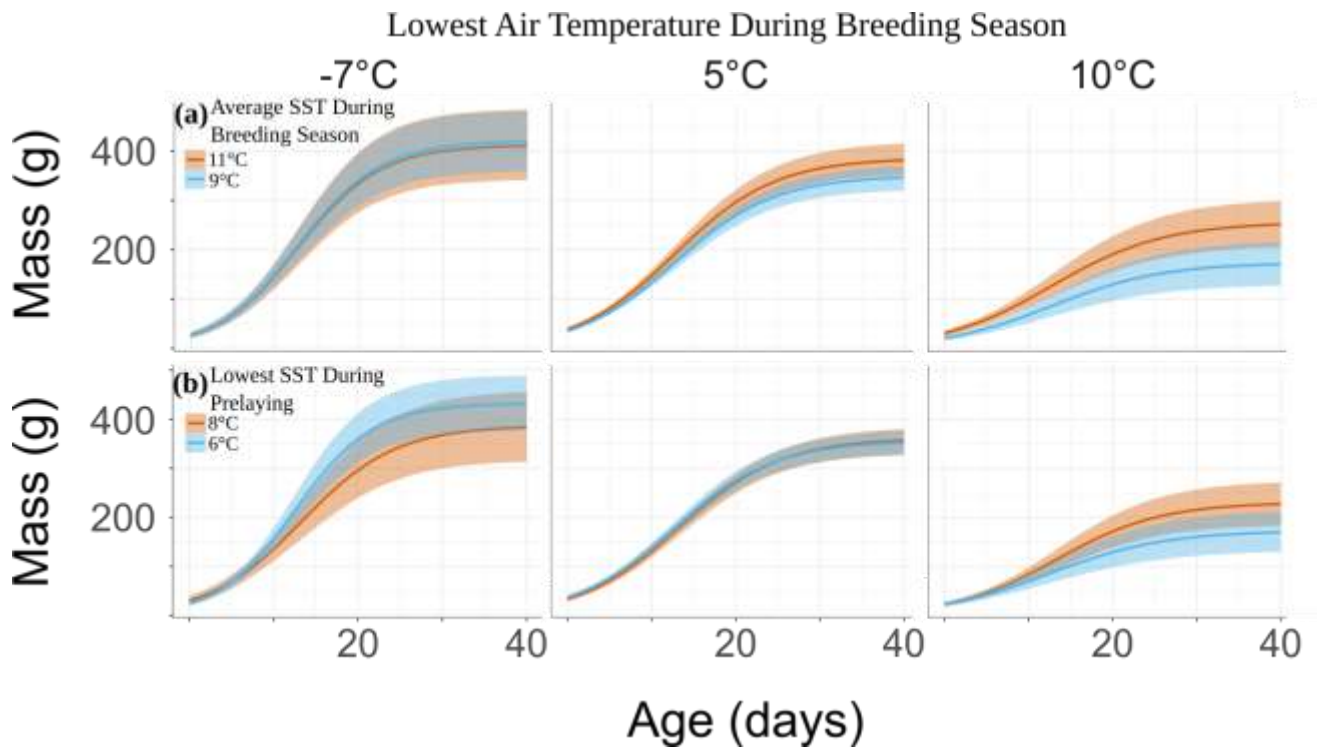
**Figure 3.1: Raw annual growth curves for each year of the study for A) Alpha unfed kittiwakes, B) Beta unfed kittiwakes, C) Alpha fed kittiwakes, and D) Beta unfed kittiwakes.**

Points indicate individual weight measurements of nestlings. Points and loess curves are coloured by year of study. In two years (2016 & 2017) no mass measurements beyond 30 days of age were taken for beta nestlings. See Appendix A figure S2 for a plot of the unified Richards curves fit to the data across years (Appendix A Fig. S2 A, B, C, D)



**Figure 3.2: Interaction between the number of days an unfed alpha nestling overlapped its growth with a beta sibling and a) the average air temperature in a season and b) the average sea-surface temperature of a season.**

See Appendix A Table A15 for full model details.



**Figure 3.3: Impacts of variation within air temperature and sea-surface temperature (SST) windows on the growth of unfed beta nestlings.**

In the display of interactions only the range of SST and air temperature that occurred in a given year are shown. Both A & B display an effect of different minimum air temperatures from a particularly cold minimum temperature breeding season on the left most panel to a warm minimum air temperature breeding season on the right. Within each panel effects of A) different average sea-surface temperatures during the breeding season or B) the minimum sea-surface temperature during the pre-laying period are displayed. See Appendix A Table A13 for full model details.

**Table 3.1: Hypotheses (H) and predictions (P) tested in the present study, with the associated statistical test and result tables and figures.**

<b>Hypothesis or prediction</b>		<b>Test or Result</b>
<b><i>H1</i></b>	<b><i>Traits expressed early in growth are more influenced by environmental conditions before hatching than by conditions after hatching</i></b>	<b>Sliding Window Analysis &amp; Environmental Models of Growth</b>
P1.1	Windows identified in our model selection process will be earlier for growth rate and timing of maximum growth than for the asymptote	Table 3.2; Appendix A Table S8
P1.2	Confidence intervals of the estimated effects of environmental windows will not overlap zero in environmental models of growth.	Table 3.3; Appendix A Tables A12 - A16
<b><i>H2.1</i></b>	<b><i>Warmer sea-surface temperatures result in conditions that make nestling growth poor</i></b>	<b>Environmental Models of Growth</b>
P2.1	Warmer sea-surface temperatures are associated with decreased growth rates, lighter asymptotes, and later timing of maximum growth in environmental models of growth.	Figs. 3.2, 3.3 Appendix A Tables A12 to A16
<b><i>H2.2</i></b>	<b><i>Colder air temperatures result in poor nestling growth</i></b>	<b>Environmental Models of Growth</b>
P2.2	Colder air temperatures are associated with decreased growth rates, lighter asymptotes, and later timing of maximum growth in environmental models of growth.	Figs. 3.2, 3.3; Appendix A Tables A12 to A16
<b><i>H2.3</i></b>	<b><i>Increased food availability increases the energy budget of nestlings allowing them to maintain growth under variable environmental conditions</i></b>	<b>Environmental Models of Food-Supplemented Nestlings &amp; Interaction Terms</b>
P2.3.1	Food-supplemented nestlings are less affected by air temperature during growth.	Appendix A Figs. A9, 10; Appendix A Table A14
P2.3.2	Interaction terms between sea-surface and air temperature in non-food-supplemented nestlings do not overlap zero, and the effects of air temperature are lessened when sea-surface temperatures are cold.	Fig. 3.3; Appendix A Tables A12, A13
<b><i>H3</i></b>	<b><i>Alpha nestlings that have to compete with beta siblings expend more energy, which makes them more sensitive to environmental conditions</i></b>	<b>Environmental and Sibling Overlap Models of Alpha Nestling Growth</b>
P3	Interaction terms between environmental windows and the number of days an alpha nestling shares its nest with a beta nestling do not overlap with zero and suggest increased effects of the environment with increased overlap	Fig. 3.2; Appendix A Fig. A10; Appendix A Tables A15 & A16

**Table 3.2: Environmental windows retained in our environmental analysis.**

Windows that overlapped multiple categories are indicated by a slash (e.g. Incubation/Growth indicates a window that spans incubation & growth). Displayed are windows identified for air and sea-surface temperature (SST) for kittiwakes that were not food-supplemented and those that were food-supplemented. For full model comparison statistics see Appendix A table S8.

<b>Not food supplemented</b>				
<b>SST</b>		<b>Asymptote</b>	<b>Max Growth Rate</b>	<b>Timing of Max Growth</b>
	Alpha	Growth*	Prelying	Prelying
	Beta	Breeding Season*	Prelying*	Prelying
<b>Air Temperature</b>				
	Alpha	Breeding Season*	Prelying	Prelying
	Beta	Incubation/ Growth	Prelying	Breeding Season*
<b>Food Supplemented</b>				
<b>SST</b>		<b>Asymptote</b>	<b>Max Growth Rate</b>	<b>Timing of Max Growth</b>
	Alpha	Growth	Breeding Season	Prelying
	Beta	None	Prelying	Breeding Season
<b>Air Temperature</b>				
	Alpha	Growth	Growth	Prelying/ Incubation*
	Beta	None	Prelying	Prelying

\* Indicates windows for which the effect was retained in our environmental model for the growth of this nestling group.

**Table 3.3: Summarized impacts of air and sea-surface temperature on nestling kittiwake growth.**

	Alpha		Fed	Beta	
	Fed	Unfed		Unfed	
<b>Warm SST</b>	-	Lighter asymptote	-	Heavier asymptote, faster maximum growth, & earlier timing of maximum growth*	
<b>Cold SST</b>	-	Heavier asymptote	-	Lighter asymptote, slower maximum growth, & later timing of maximum growth*	
<b>Warm Air</b>	Later timing of maximum growth	Heavier asymptote	-	Lighter asymptote, slower maximum growth, & later timing of maximum growth	
<b>Cold Air</b>	Earlier timing of maximum growth	Lighter asymptote	-	Heavier asymptote, faster maximum growth, & earlier timing of maximum growth	

\*Effect only apparent under warm air temperatures and when compared to cold or warm sea-surface temperatures under the same conditions. Model predictions suggest air temperatures have the largest impact.

### 3.6 References

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## Chapter 4

# Shifting environmental predictors of phenotypes under climate change: a case study of growth in high latitude seabirds

### 4.1 Abstract

Climate change is altering species' traits across the globe. To predict future trait changes and understand the consequences of those changes, we need to know the environmental drivers of phenotypic change. In the present study, we use multi-decadal long datasets to determine periods of within-year environmental variation that predict growth of three seabird species. We evaluate whether these periods changed over time and use them to predict future growth under climate change. We find that predictions of trait change could be improved by considering that 1) the *timing* of environmental factors used to predict traits (predictive-environmental features) can change over time, and 2) the *type* of predictive-environmental features can change over time. We find evidence of changes in the *timing* of environmental predictors in all populations studied and evidence for a change in the *type* of predictor in the studied Arctic murre population. Environmental models of growth predict that warming conditions will decrease growth rates and bird body sizes in two species (black-legged kittiwake *Rissa tridactyla* and glaucous-winged gull *Larus glaucescens*), but not the third (thick-billed murre *Uria lomvia*). Consequently, climate change is likely to decrease fledging rates in the gulls and kittiwakes. Further, we find that ice-cover historically predicted murre chick growth well, but no longer does – instead air temperature is now a better predictor of murre growth. Our study highlights a need to investigate whether environmental determinants of trait variation commonly shift in a changing climate and whether such changes have implications for adaptation to novel environments.

### 4.2 Introduction

The relationship between an organism's phenotype and its environment is fundamental to ecology and evolutionary biology (West-Eberhard 2003; Sultan 2015), as the expression of a particular phenotype in

response to environmental conditions (plasticity) can shape both the fitness of an organism and the demography and evolution of a population (Ghalambor et al. 2007; Vedder et al. 2013; Snell-Rood et al. 2018; Rescan et al. 2020). Yet, we are far from accurately predicting phenotypic, demographic, or fitness changes in response to climate change for many species and traits. Early life in particular is often a strong selective period, during which many organisms integrate environmental information into a canalized adult phenotype (Williams 1957; Hamilton 1966; English et al. 2016). Therefore, measuring the relationship between early-life phenotypes and environmental conditions is essential in determining the role of the environment in shaping the diversity of phenotypes in a population. Furthermore, environmental change is likely to produce novel environments that may alter patterns of selection experienced during early life and result in reduced recruitment.

In the event of novel environmental conditions in the future, we need to know if we can predict organisms' responses to environmental change, and whether the responses will be adaptive (English et al. 2016; Snell-Rood et al. 2018; Bonamour et al. 2019; Simmonds et al. 2019). The population responses to new environments will likely be caused by a complex mix of micro-evolution and phenotypic plasticity. Understanding the associations between environment and early-life growth phenotypes is an important first step in identifying potential sources of selection or cues for plasticity (Ghalambor et al. 2007; Sultan 2015). After identifying new predictors of traits in longitudinal studies, researchers can evaluate hypotheses related to how these predictors might drive phenotypic change.

The effects of the environment on the developing phenotype can be complex and may include direct effects and indirect effects acting via interactions with other individuals such as parents (Noble et al. 2018; Sauve et al. 2021). Moreover, environmental effects may operate at particular stages, characterized by specific time windows (Kruuk et al. 2015; van de Pol et al. 2016; de Zwaan et al. 2020). The availability of multi-decadal datasets and the development of sliding window statistical approaches are timely assets to identify critical time windows during which particular environmental effects occur (Simmonds et al. 2019).

High latitude populations are ideal study systems in this regard because they are experiencing rapidly warming temperatures that could impact growth directly through overheating, and indirectly through ecosystem changes (Hatch 2013; Gaston and Elliott 2014; Piatt et al. 2020; Choy et al. 2021). Here we investigate the relationship between early-life environmental conditions and growth, a trait frequently associated with immediate and future survival, in three high latitude seabirds. We had four objectives: 1) identify time windows and environmental variables (e.g. air temperature, sea ice-cover [hereafter ice-cover]) within the breeding season that predict offspring growth, 2) determine if these environmental variables change across years, 3) determine whether the timing of these predictive windows change across years, and 4) use this knowledge to make predictions about offspring growth under future climate change. Because environmental conditions are changing quickly in high latitude areas (Moon et al. 2021), we expected that the timing of environmental growth predictors or the predictors themselves might differ between historical and contemporary periods.

## **4.3 Methods**

### **4.3.1 Species, study sites, and available data**

We used growth data from long-term studies of thick-billed murres *Uria lomvia* (hereafter ‘murres’) on Coats Island, Nunavut, Canada, and glaucous-winged gulls *Larus glaucescens* and black-legged kittiwakes *Rissa tridactyla* (hereafter, ‘gulls’ and ‘kittiwakes’) on Middleton Island, Alaska (Table 4.1; Appendix B-I B1).

#### **4.3.1.1 Murres**

Each year of study on Coats Island (1986-2010; 2017-2018), chicks from ~60 parental pairs were monitored in the colony of ~15000 pairs (Table 4.1; Hipfner and Gaston 1999; Gaston et al. 2003, 2005; Gaston and Elliott 2014). One hundred murre eggs were marked during incubation and visited every two days to determine hatching date. If a chick was found wet, it was recorded as hatching on the date of the check and, if a chick was pipping, it was recorded as hatched the

following date. If no information was available, a chick was aged using wing length measurements such that the hatch date was recorded as the date of discovery, the previous date, and two days prior if the wing length was less than or equal to 25mm, 26-27mm, and 28-29mm, respectively. Individuals were banded upon hatching or toe-clipped (if too small to band) and subsequently banded. Chicks were weighed every two to four days. Only mass up to 14 days of age was analyzed because chicks begin to depart from the colony at 15 days, so masses before 15 days of age are unbiased by departure age.

#### 4.3.1.2 Gulls

Two gull plots (each ~1000m<sup>2</sup>, and encompassing 50-100 nests) were monitored each year of study (2002-2010; 2012; 2016-2018; total population on Middleton ~10,000 birds, [Denlinger 2006]). Gull nests were marked and checked every four days to determine approximate laying and hatching dates. If a chick was found wet it was recorded as hatching on the date of the check, but if a chick was dry the hatch date was recorded as the mid-point date between check dates. Finally, if a chick was pipping the hatch date was recorded as date after the check. Chicks were banded with a temporary plastic band with a short letter and number sequence to identify individuals. Attempts were made to capture chicks every four days after first discovery, but because chicks can wander from the nest soon after hatching and some chicks avoid capture, the majority of chicks were not weighed at each four-day interval (~2.2 measurements taken per chick; Table 4.1).

#### 4.3.1.3 Kittiwakes

On Middleton Island, ~60-400 breeding pairs of kittiwakes that were part of a larger colony of ~15000 birds were monitored annually in an abandoned radar tower (Gill and Hatch 2002). Birds at the radar tower construct their nests on wooden shelves that have been built in parallel rows on

the exterior of the tower. One-way glass panel windows are set in the interior of the tower and can be used to observe each nest from within the tower, and can be removed to handle nestlings. Nests were checked twice daily (9:00 and 18:00 h) throughout the season to record laying and hatching. Eggs hatch asynchronously within clutches, with an average difference of ~1.6 days between the first and second laid egg (Merkling et al. 2014). In each year of the study, the first-hatched and second-hatched chicks were marked with a nontoxic colour marker to distinguish chick rank, and were banded at five days post-hatch for individual identification. Chicks were weighed every five days from hatching to 40 days (i.e., close to fledging). Mass was weighed to the nearest 0.1 g using an electronic scale. As several experiments have been conducted on the nests in the past (Merkling et al. 2016), we excluded data from any chicks that had been experimentally manipulated.

#### **4.3.2 Environmental variables**

We evaluated three environmental variables that potentially influence chick growth for some or all seabird datasets: 1) sea-surface temperature, because it frequently reflects the community composition and abundance of prey species for seabirds (Furness 2016); 2) air temperature, because it could improve or worsen thermal conditions for growing chicks, it is associated with growth in kittiwakes (Sauve et al. 2022), and warm temperatures contribute to egg-losses and adult mortality in murrelets at Coats Island (Gaston and Elliott 2013); and 3) sea ice cover (for murrelets), because it is an indicator of a regime shift in the marine ecosystem near Coats Island and has been associated with timing of laying and murre mass at 14-days of age (Gaston et al. 2003, 2005; Gaston and Elliott 2014). We ran analyses for ice cover, sea-surface temperature, and air temperature for murrelets, but only present results for ice-cover and air temperature in the

main text because ice-cover and sea-surface temperature are closely correlated in the spring before and during ice breakup (Appendix B-II).

Because we expected that sea-surface temperature and ice-cover affect prey availability, we used sea-surface temperature and ice-cover variables averaged across an area that approximately reflects the foraging range of each species. For murres all pixels within 60 km of Coats Island were averaged each day for ice-cover. For kittiwakes and gulls, all pixels within 100 km or 50 km respectively of Middleton Island were averaged each day for sea-surface temperatures (Mallory et al. 2018). We used Version 2 of the advanced very high-resolution radiometer dataset (AVHRR) daily sea-surface temperature or sea-ice concentration data from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC; <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.OISST/.version2/.AVHRR/>). Air temperatures for Coats Island were collected from the Coral Harbour weather station (~100 km from the murre growth plots; [https://climate.weather.gc.ca/index\\_e.html](https://climate.weather.gc.ca/index_e.html)). Elliott & Gaston (2015) found that daily maximum and minimum air temperature at Coats Island and Coral Harbour are correlated ( $R^2 = 0.6$  for both parameters), suggesting that air temperatures at Coral Harbour may be used as a proxy for conditions at Coats Island. Air temperatures for Middleton Island were collected from an airport weather station situated ~2 km from the kittiwake radar tower and gull plots (<https://www.ncdc.noaa.gov/cdo-web/cart>).

### **4.3.3 Statistical Analyses**

#### **4.3.3.1 Models of growth**

We modelled all growth patterns using Bayesian mixed models with the R package ‘brms’, which uses the ‘Stan’ software (Bürkner 2017; Stan Development Team 2019). In all models, we

added chick identity and year as random effects for each growth parameter. For all analyses, our biological traits of interest were the individual deviations from the mean population-level estimates of growth curve parameters (for murre; *Intercept* and *Slope*; for kittiwakes and gulls, *Asymptote*, *maximum growth rate*, and *timing of maximum growth rate*). Because we only used data from the approximately linear part of the growth curve for murre, we modelled murre growth as a linear function of age, the parameters of interest being the intercept and slope of the regression. We used linear mixed models for murre with a fixed effect predictor of age. Age in days was population mean centred for murre so that the intercept of the regression is the estimated mean mass of a chick during growth and the slope is the estimated mean daily mass change. Because the data span the entirety or most of the chick growth phase for kittiwakes and gulls, we used non-linear mixed models (the unified Richard's curve) for gulls and kittiwakes. The unified Richard's curve is a reparameterization of the Richard's curve, which is a generalized version of a logistic function providing estimations of the relative maximum growth rate, the age at maximum growth, and the asymptote or maximum size reached during growth (Sugden et al. 1981; Tjørve and Tjørve 2017). We choose the Richard's curve because it is flexible and can take the shape of many commonly used models of determinate growth (Tjørve and Tjørve 2017). Details of model priors, the extraction of individual deviations, and an analysis of temporal changes in growth parameters are provided in Appendix B-III.

#### 4.3.3.2 Sliding window analyses

We performed sliding window analyses using the R package 'climwin' (van de Pol et al. 2016). A sliding window analysis identifies a time window for which an environmental variable of interest best explains variation in a measured biological trait. We used relative windows that assume each individual record will be impacted by climate at different times relative to the timing of the

biological trait. The sliding window analysis varies the start and duration of windows in increments of days. We used it to compare linear and quadratic relationships between the mean, minimum and maximum values of climate for a given time window and individual estimates of model parameters. We evaluate air temperature, ice-cover (murre only), and sea-surface temperature for murre, gull, and kittiwake in a time-period up to 100, 150, and 120 days before measurement of chicks, when they would be 14, 50, and 40 days old (roughly fledging date), respectively. The lengths of our time periods were chosen to encompass prelaying, follicle development, incubation, and growth (Roudybush et al. 1979; Astheimer and Grau 1990). For our interpretation of windows, we have binned the windows identified by our analysis into these time periods. Our process of selection for *climwin* models can be found in Appendix B-III.

#### 4.3.3.3 Environmental models of growth

The climatic windows identified by *climwin* were fitted in a model that estimated the statistical effects of each window on all growth curve parameters. If an identical window was detected for two or more growth parameters, the effect of that window was only evaluated once in the growth models. First, we ran separate models for air temperature, sea-surface temperature (gull and kittiwake only), and ice-cover (murre only). Finally, we ran a model that retained only fixed effects with credible intervals that did not span zero in sea-surface and air temperature models, and combined them into one model. We used an information criterion (LOOIC) derived from approximate leave-one-out cross-validation using Pareto-smoothed importance sampling to compare and evaluate the predictive performance of a model (PSIS-LOO [Vehtari et al. 2017]). Models with a difference in LOOIC values  $>5$  were considered improvements in model fit.

#### 4.3.3.4 Timing changes in determinant windows between historical and contemporary periods

We evaluated whether windows detected by the sliding window analysis changed throughout the study period for each species. To do this, we ran the sliding window described above but ran the analyses on each dataset split into two subsets (Appendix B-I Table B1). For each dataset we call the older subset the ‘historical’ period and the more recent subset the ‘contemporary’ period. We split the Coats Island dataset: 1) before and after 1995, corresponding to a marked discontinuity in sea ice and food web characteristics (Gaston and Hipfner 1998; Gaston et al. 2012; Provencher et al. 2012), and 2) before and after 1999 to compare the 1995-split to an analysis of the data subsets with similar sample sizes. The ocean regime near Middleton Island is more cyclical than that at Coats Island (Hatch 2013). Consequently, we only split the kittiwake and gull datasets from Middleton once to retain roughly equal sample sizes in the historic and contemporary periods (Appendix B-I B1). If we retained a window in both the historical and recent data subsets, we compared the median start and end of the top 95% models for that variable (sea-surface temperature, air temperature, or percentage ice-cover). The top 95% of models are those that, when their Akaike weights are summed, encompass 95% of the sum of all Akaike weights for models evaluated in the sliding window analysis (Bailey & van de Pol, 2016; van de Pol et al., 2016). If the median start and end dates did not overlap between the two data subsets, we considered this support for a shift in the time period of environmental variation that best predicts chick growth. For all data subsets (historical, contemporary, and across the entire dataset) we calculated Bayes  $R^2$  from linear models run in ‘brms’ with each growth parameter as the response and all windows identified for a specific subset by our sliding window analysis as predictors (Gelman et al. 2018).

#### 4.3.3.5 Predicting Future Growth

We used the environmental growth models to make predictions about chick growth in a hypothetical environment altered by climate change. We made predictions based on future scenarios of high and low emission for 2080 (Intergovernmental Panel on Climate Change 2018). The low emissions future corresponded to a 2.2°C increase in air temperatures, a 0.75°C increase in sea-surface temperatures and a 30% decrease in ice-cover. The high emissions future corresponded to an 8.3°C increase in air temperatures, a 1.25°C increase in sea-surface temperatures and a 70% decrease in ice-cover for murre. All air temperature and ice-cover predictions are estimates derived from Collins et al. (2014) and correspond to estimates for ~60°N latitudes in the year 2080. Sea-surface temperature predictions are estimates derived from Ruela et al. (2020) and correspond to estimate changes predicted in the Gulf of Alaska. The low emission future corresponds to warming under representative concentration pathway 2.6 (RCP2.6; path required to keep global warming below 2°C), and the high emission future corresponds to warming under representative concentration pathway 8.5 (RCP8.5; unimpeded emissions scenario).

## **4.4 Results**

### **4.4.1 Changes in growth over time**

On average, murre chicks were larger at the end of the study but did not have a clear change in growth rate over the course of study (Fig. 4.1a, Appendix B-I table B3). Gull chicks in the latest years tended to reach the lightest asymptote (Fig. 4.1b). The timing of maximum growth in gulls was non-linear such that chicks growing in the middle of the study were starting maximum growth at ~18-20 days of age, while chicks at the end and beginning of the study started maximum growth at a ~13-15 days of age (Fig. 4.1b, Appendix B-I table B4). On average, both first-hatched and second-hatched kittiwakes grew more slowly, started maximum growth at an

older age, and reached a lighter asymptote at the end of the study compared to the beginning (Fig. 4.1c, d, Appendix B-I table B5).

#### **4.4.2 Climate and growth**

In breeding seasons with a higher maximum ice-cover, murre chicks grew more quickly (Fig. 4.2a, b), and when maximum air temperatures were warmer during the incubation/growth period, murres tended to grow more quickly as well (Fig. 4.2c, d). Warmer conditions were associated with slower growing and smaller gull chicks, and second-hatched but not first-hatched kittiwake chicks. Gulls grew more slowly and started maximum growth at an older age when maximum air temperatures during incubation and growth were warmer (Appendix B-I table B14). None of the environmental models for growth in first-hatched kittiwakes improved model fit compared to the baseline model (Appendix B-I table B7). Second-hatched kittiwakes grew more slowly, started maximum growth at an older age, and reached a lower asymptote when maximum air temperatures during the breeding season were warmer (Fig. 4.3).

#### **4.4.3 Changes in windows over time**

In all three species, we found evidence of temporal shifts in the timing of predictors identified by our sliding window analysis (Fig. 4.4, 4.5, 4.6). Variation in murre growth parameters was better explained by environmental windows in contemporary periods, while in gulls and kittiwakes there was heterogeneity across growth traits in variation explained by windows in historic and contemporary periods (Table 4.2). The periods of ice-cover identified by the sliding window analysis of average murre mass tended to be similar before and after 1995, but for growth rate the windows shifted from the prelaying period to encompass follicle development and incubation after 1995 (Fig. 4.4a). The periods of air temperature identified by the sliding window analysis shifted from the incubation and growth period to the prelaying stage after 1995 (Fig. 4.4b). In the

data subset of murre growth encompassing 1986 to 1994, only ice-cover windows were retained as predictors of chick growth, and only a single air temperature window was retained in the analysis of murre growth after 1994 (Fig. 4.4a, b).

Sea-surface temperature windows that predicted maximum growth rate and timing of maximum growth rate remained similar before and after 2009 for gulls (Fig. 4.5a). The sea-surface temperature window that predicted the asymptote of gull mass shifted from prelaying/incubation to the growth period after 2008. Only the window of sea-surface temperature that predicted the asymptote was retained for the model of gull growth before 2009, while no windows of sea-surface temperature were retained in the model of gull growth after 2009 (Fig. 4.5). Windows of air temperature that predicted maximum growth encompassed prelaying before and after 2009 but shifted to later in the prelaying period after 2009. The air temperature window that best predicted the timing of maximum growth shifted from the prelaying to growth period (Fig. 4.5b).

Sea-surface temperature windows that best predicted the timing of maximum growth rate and maximum growth rate of first-hatched kittiwakes shifted from intervals during incubation and growth to a prelaying period after 2007 (Fig. 4.6a). Air temperature windows that predicted growth parameters of first-hatched kittiwakes remained similar except for windows that predicted the timing of maximum growth, which shifted from a period during growth to a period during prelaying. None of the windows identified in the sliding window analysis for any data subset were retained in the model selection for growth of first-hatched kittiwakes (Fig. 4.6a, b). Almost all sea-surface and air temperature windows that predicted maximum growth or timing of maximum growth in second-hatched chicks tended to overlap or encompass the same growth periods (Fig. 4.6c, d). However, similarly to first-hatched chicks, the sea-surface temperature

windows that best predicted maximum growth and timing of maximum growth shifted to the prelaying period after 2007 in second-hatched kittiwake chicks (Fig. 4. 6b).

#### **4.4.4 Prediction of future growth**

Under high emission scenarios, large impacts of climate change on growth are predicted for gulls and second-hatched kittiwakes. No environmental windows were retained for models of growth for first-hatched kittiwakes, limiting our ability to make predictions about first-hatched kittiwake chicks in a warming environment (Fig. 4.6a, c). Under a scenario of high effort to reduce emissions (RCP2.6), the models predicted little impact of warming on chick growth of murrelets, gulls, or second-hatched kittiwakes (Fig. 4.7). Under high emissions (RCP8.5), the models predicted limited effects on murrelets (Fig. 4.7a) and a greater effect on the growth of gulls and second-hatched kittiwakes (Fig. 4.7b, c). The models suggest that warming conditions under a high emissions scenario will result on average in slower growing and lighter asymptotic masses for gulls and second-hatched kittiwakes.

### **4.5 Discussion**

We applied sliding window analyses combined with long-term growth data to identify specific windows of environmental variation associated with growth of three seabird species. We found 1) windows during the breeding season that predict variation in growth for each species, 2) that the environmental variable that best predicts growth can change over time, 3) that the period during which an environmental variable is the best predictor of a growth parameter might also change over time, and 4) that future warming should result in poorer growth for gulls and kittiwakes, but not murrelets.

#### **4.5.1 Biological interpretation of associations between environmental windows and growth**

More extensive ice-cover during the prelaying period and warmer air temperatures during incubation/growth periods were associated with faster growth in murre chicks. These results are similar to what has been identified through previous analyses of the Coats Island dataset on murre. When ice-extent is the lowest in Hudson's Bay, the chicks tend to grow more slowly, presumably because ice extent is associated with abundance of preferred prey (artic cod *Boreogadus saida*) in the murre diet (Gaston et al. 2005). Warmer air temperatures might improve thermal conditions for growing chicks, as observed in some other high latitude bird species (McKinnon et al. 2012). But, the benefits of warmer air conditions may be transitory, as adult murre are thought to overheat quickly under excessive heat conditions (Choy et al. 2021). Alternatively, the positive relationship between air temperature and murre growth could reflect increased abundance of the subarctic capelin *Mallotus villosus* that are associated with the 'Atlantification' of North Eastern Hudson's Bay (Provencher et al. 2012).

We found a weak quadratic relationship between the growth rate of gulls and sea-surface temperatures during the prelaying period, which suggested that warm or cold sea-surface temperatures could result in faster growing chicks (Appendix B-I table B28). We generally assumed warmer sea-surface temperature conditions are associated with poor foraging near Middleton, but gulls have broad diets and might do well foraging in intertidal zones, scavenging, and preying on conspecifics when sea-surface temperatures are warm (Hayward et al, 2020). Consistent with that scenario, the sea-surface temperature during the prelaying period was the best predictor of growth rate (Appendix B-I table B14). Offspring grow more quickly to a smaller size under warm sea-surface temperatures and warmer air temperatures are associated with smaller asymptotes and a later timing of maximum growth in gull chicks, suggesting

parents might also alter investment (e.g. via hormones or egg size, Grootuis et al. 2005; Hipfner 2012; Appendix B-I table B28).

Similar to an earlier analysis on Middleton Island kittiwakes, our results suggest that warmer air temperature predicts poorer growth for second-hatched nestlings (Sauve et al. 2021). Because the observed temperatures did not exceed the thermal neutral zone of kittiwake chicks (Bech et al. 1984), we hypothesize that the air temperature during the breeding season predicts or is associated with favourable or unfavourable ecological conditions correlated with temperatures rather than a direct effect of air temperature on nestlings (e.g. colder conditions are associated with an increase in capelin; Hatch 2013).

#### **4.5.2 Changing predictors of growth across time periods**

As global warming induces rapid environmental changes, the environmental predictors of traits can change among years. When testing whether the environmental variables can change over time, we found that ice-cover was previously an important predictor of murre growth but may no longer be (Fig. 4.4; Appendix B-I table B7). The change in ice-cover as the main predictor of growth matches observations that the ecosystem on Coats Island is shifting from an ice-dominated ecosystem to one that is more similar to the Atlantic (Gaston and Hipfner 1998; Gaston et al. 2012; Provencher et al. 2012; Gaston and Elliott 2014).

We did not find evidence for a change in the environmental variables that best predict growth in gulls or kittiwakes (Fig. 4.5, 4.6). The gull and kittiwake data encompass warm and cool breeding seasons with less of a discontinuous shift in the ecosystem than at Coats Island (Gaston et al. 2012; Hatch 2013). Conditions in the Gulf of Alaska are dominated by the Pacific Decadal Oscillation, which alternates between decades-long phases of cool, wet conditions and warmer, drier conditions (Mantua and Hare 2002). Future studies should try to identify periods

of oceanographic and weather conditions that best predict growth across warm years only, to determine when variables are predictors of seabird growth during marine heatwaves.

#### **4.5.3 Temporal changes in the timing of growth predictors**

Previous studies have demonstrated that the timing of environmental variables predicting avian phenological events can differ among habitats (e.g. Bonamour et al., 2019), but to the best of our knowledge whether the timing of predictors shifts over time has not been evaluated. Shifts of windows may be of concern because they may lead parents to follow unreliable cues and lead to maladaptive timing or offspring number (Temme & Charnov 1987; Visser et al. 2006). In our case study, shifts in growth windows to earlier in the season could indicate offspring reduction is determined early, while windows later in the season could indicate abrupt changes occurring later in the breeding season (conditions are more frequently unfavourable late in the season). Abrupt deterioration of breeding season conditions is expected to occur more frequently as late season anomalies and heat-waves are expected to become more common (e.g. Piatt et al. 2020).

The timing of the determinants of growth changed over time for all three species studied (Figs. 4.4, 4.5, 4.6). We did not identify a general pattern in the direction of these shifts within the breeding season. Across all three species, we observed environmental windows that moved to earlier periods in the breeding season (e.g. shifted from incubation and growth to prelaying) but also other shifts to later periods (e.g. from prelaying to chick rearing). Growth is a function of parental and chick energy budgets. Predictors identified prenatally could imply indirect parental effects (e.g., egg size, hormones, incubation) while predictors during the postnatal period might suggest impacts of environmental conditions on brooding, foraging rates, or the chick thermal environment (Andrew et al. 2017; Andreasson et al. 2018; Sauve et al. 2022), but importantly should be confirmed with experimental approaches (Andrew et al. 2017).

#### **4.5.4 Implications of shifting predictors: cues and constraints**

Some of the observed associations between climate and chick growth could be the result of growth responses to environmental cues. Adaptive responses to changing environmental conditions are facilitated by temporal autocorrelation. When this autocorrelation is high, conditions in one period can be used to predict conditions in another when natural selection is experienced (Gavrilets and Scheiner 1993; de Jong 1999). To determine if the associations we detected allow adaptive responses, we need to know whether they predict future environments (i.e., can the parent environment predict the chick environment or can the chick environment predict the adult environment?). However, we still need to know how changes caused by environmental associations affect survival and reproduction. Empirical work has demonstrated that reproductive hormones and parental care are adjusted to food conditions, number of offspring, partner effort, and prolonged pre fledging periods (Drent and Daan 1980; Jacobsen et al. 1995; Harding et al. 2009; Whelan et al. 2021).

Our analysis also illustrates some of the difficulties in identifying specific climatic windows. The sliding window analysis detected many windows, but most were not retained in our model selection process, possibly limiting our conclusions on shifts in the timing of environmental predictors. Microclimatic variation or intrinsic factors might better explain some of the variation in growth. Experimental manipulation of chick environments and continued long-term monitoring are needed to determine the importance of specific periods during ontogeny (Andrew et al. 2017; Nord and Giroud 2020; Whelan et al. 2021).

#### **4.5.5 Predicting growth in a warming world**

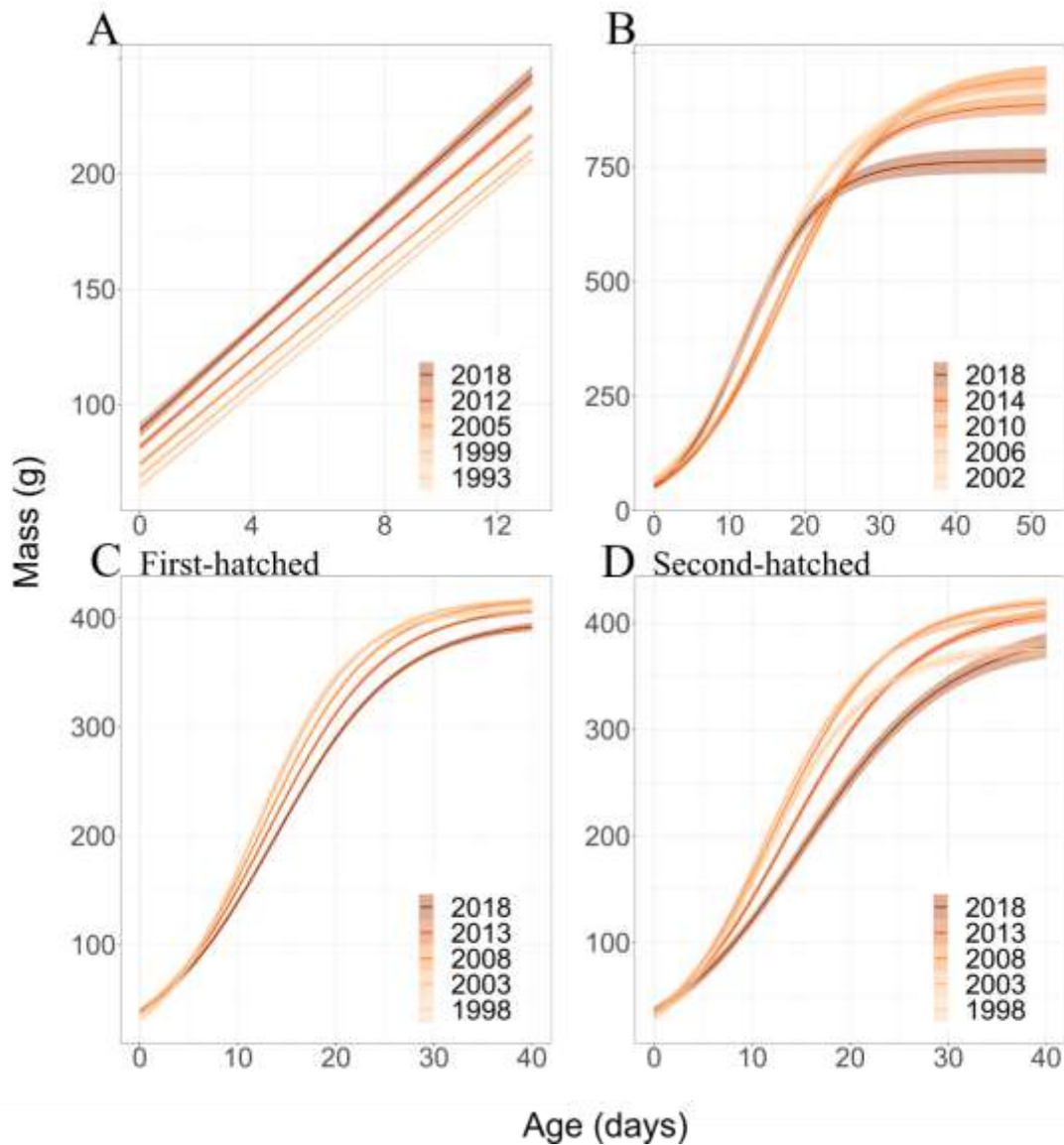
Our growth predictions qualitatively agree with some of the observed changes in murre growth and most of the observed changes in gull and kittiwake growth, suggesting that our identified

environmental periods could be driving some of the observed changes in growth across each study period (Fig. 4.7, Fig. 4.1). Our climate change predictions for murrelets suggested limited change in growth, but trends across the study period suggest heavier masses over time in murrelets. While we discuss some potential causes of the shifting windows above, the shifts highlight an important practical problem to prediction: if predictors continually change, it becomes more difficult or impossible to make long-term projections. Perhaps a more complex understanding of trait responses to fluctuating conditions is needed. For example, studies attempting to predict microevolutionary change are beginning to model selection on traits as a function of environmental conditions (Chevin et al. 2015; Gameleon et al. 2018; de Villemereuil et al. 2020). But even these models assume the same predictor of selection across years and might, like our window approach suggests, need continual updates. Further, we could not predict changes in first-hatched kittiwake growth and we hypothesize that this is because parents favour first-hatched nestlings in poor years and, therefore, growth of first-hatched kittiwakes is relatively unperturbed by the range of environmental effects measured in our study. Currently observed environments seem to have a limited impact on first-hatched kittiwakes, but future conditions could nonetheless eventually impact growth of first-hatched kittiwakes. We emphasize this as a key point and limitation for trying to predict kittiwake growth. Finally, it will be important to consider environmental conditions outside the breeding season because migratory conditions might predict unexplained variation or temporal changes in growth (e.g. Patterson et al. 2021). While previous investigations have highlighted that changes in phenology and body shape are commonly predicted responses to climate change (Parmesan 2006; Dunn and Møller 2019; Ryding et al. 2021), altered growth patterns and investment in offspring may also be common responses to climate change. Significantly, the slower-growing and smaller chicks predicted for

gulls and second-hatched kittiwakes in warm environments portend reduced survival of those chicks, as mass is often a predictor of post-fledging survival (Maness and Anderson 2013). Annual reductions in reproductive effort could have important consequences if later-hatched chicks make up a substantial proportion of the breeding population. For example, of the breeding kittiwakes on Middleton Island approximately 30% are second-hatched chicks. Thus loss of second-hatched kittiwakes could result in a reduced breeding population, if they are not replaced by first-hatched kittiwakes.

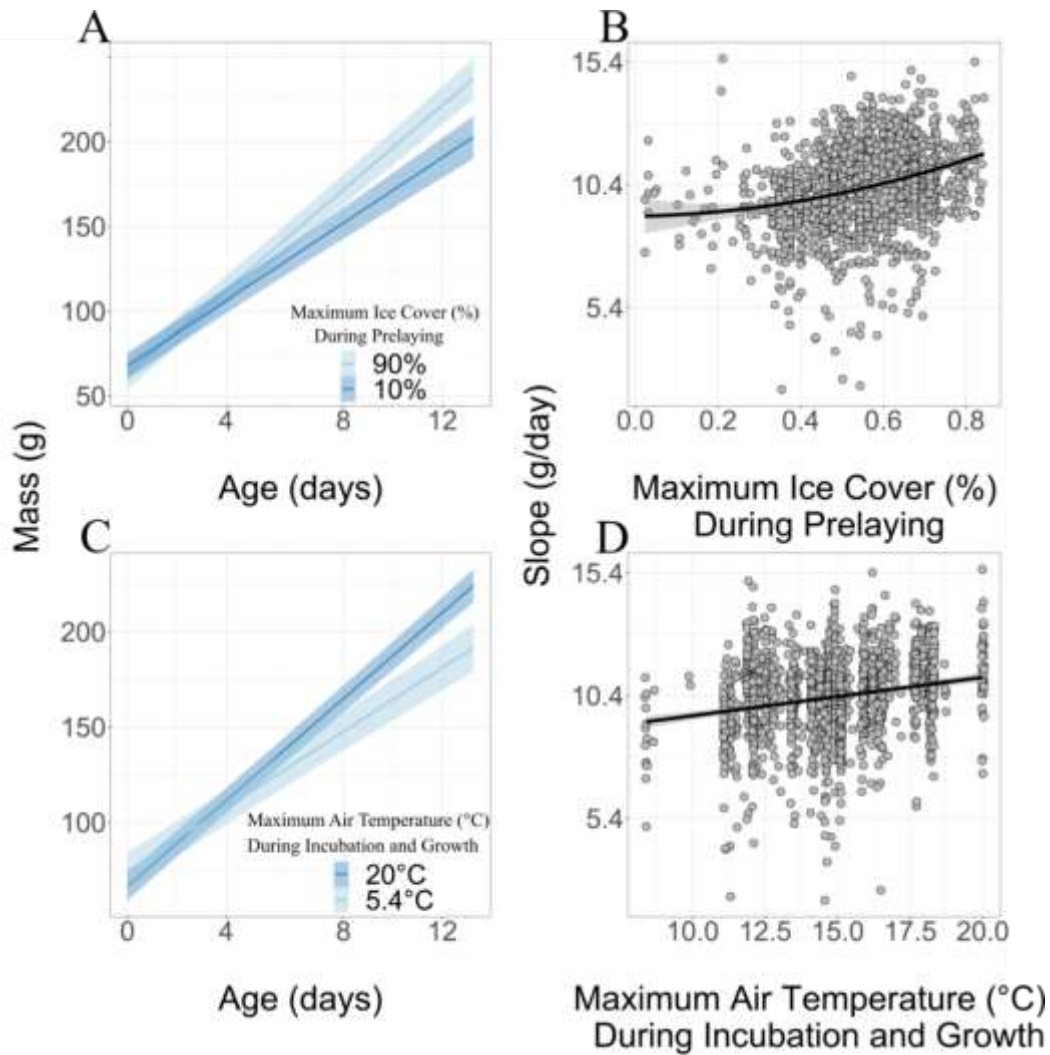
#### **4.5.6 Conclusions**

We found evidence that both the nature and timing of variables correlating with seabird growth can change over time. We identified time periods that predicted poor growth for species with multi-chick broods. We would stress, however, that the stability of environmental predictors over time is unknown, and that instability would compromise our predictive ability and the ability of species to adapt to novel conditions. There remains an important need for research that identifies temporal predictors of phenotypic traits and determines their stability under warming environmental conditions.



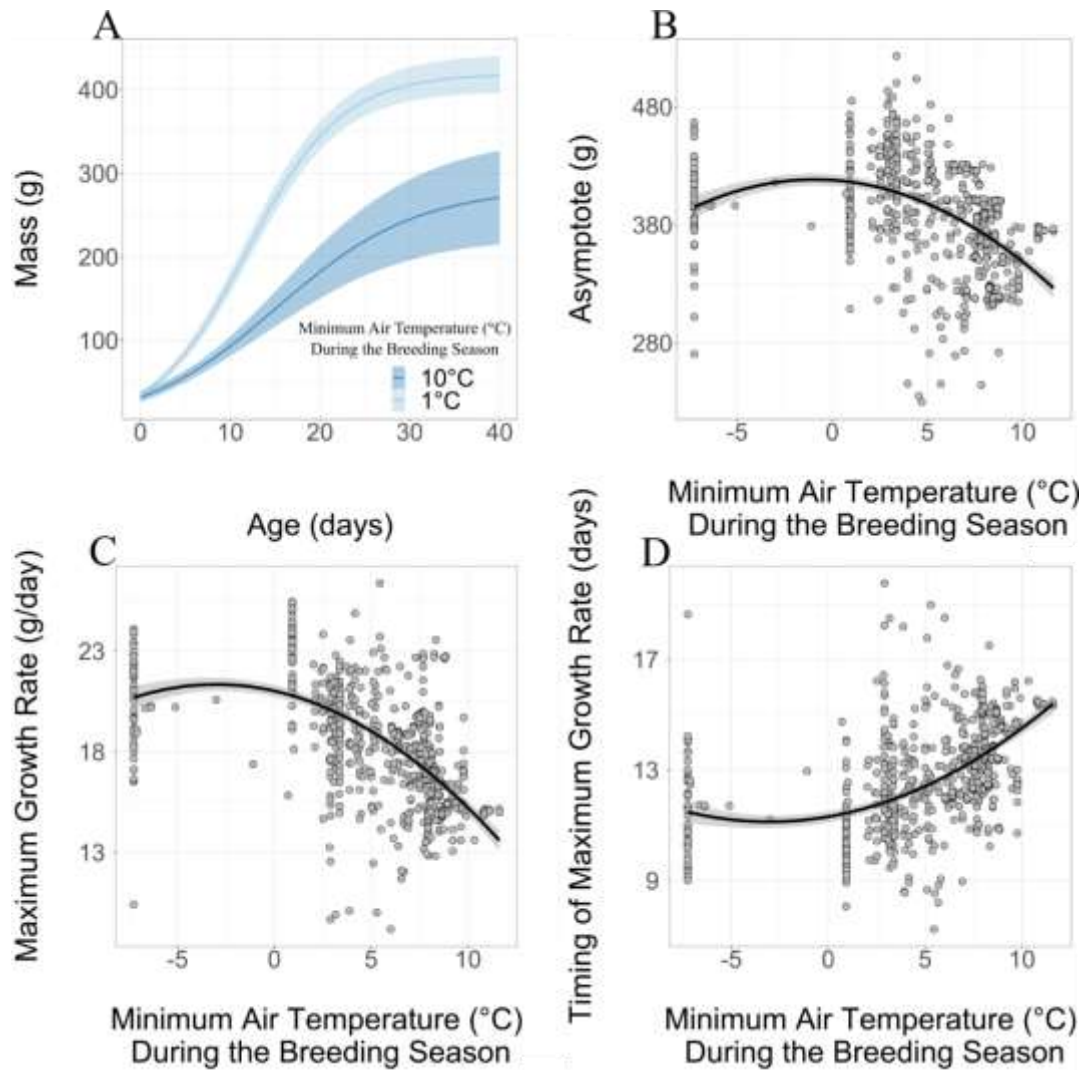
**Figure 4.1: Model predicted changes in growth over time for A) murrelets, B) gulls, C) first-hatched kittiwakes, and D) second-hatched kittiwakes.**

For each species predicted growth curves with associated 95% credible intervals (shaded areas) are displayed for the beginning and end year of each study and three evenly spaced sequential years between the start and end of the study. Details of models are presented in Appendix B-I tables B3, 4, 5, & 6.



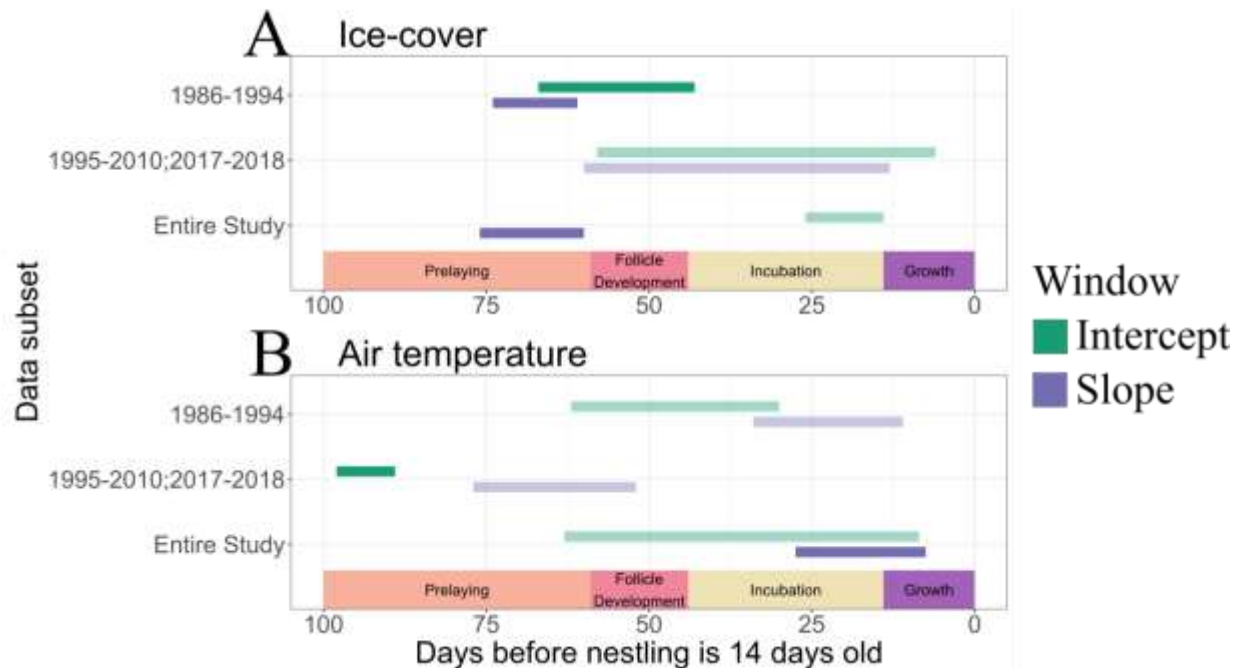
**Figure 4.2: Model predicted effects of A) maximum ice-cover during prelaying, and C) maximum air temperature during incubation and growth, and scatter plots of individual growth slopes (g/day) across B) maximum ice-cover during prelaying, and D) maximum air temperature during incubation and growth of murre chicks.**

Individual estimates in graphs on the right (B, D) are the summed annual and individual group effects estimated in our baseline linear mixed effect model and they do not account for estimate error (see Hadfield et al., 2010; Houslay & Wilson, 2017), therefore the plotted relationships are just for visualization of effects identified in our sliding window analysis. Details of the model are presented in Appendix B-I table B23.



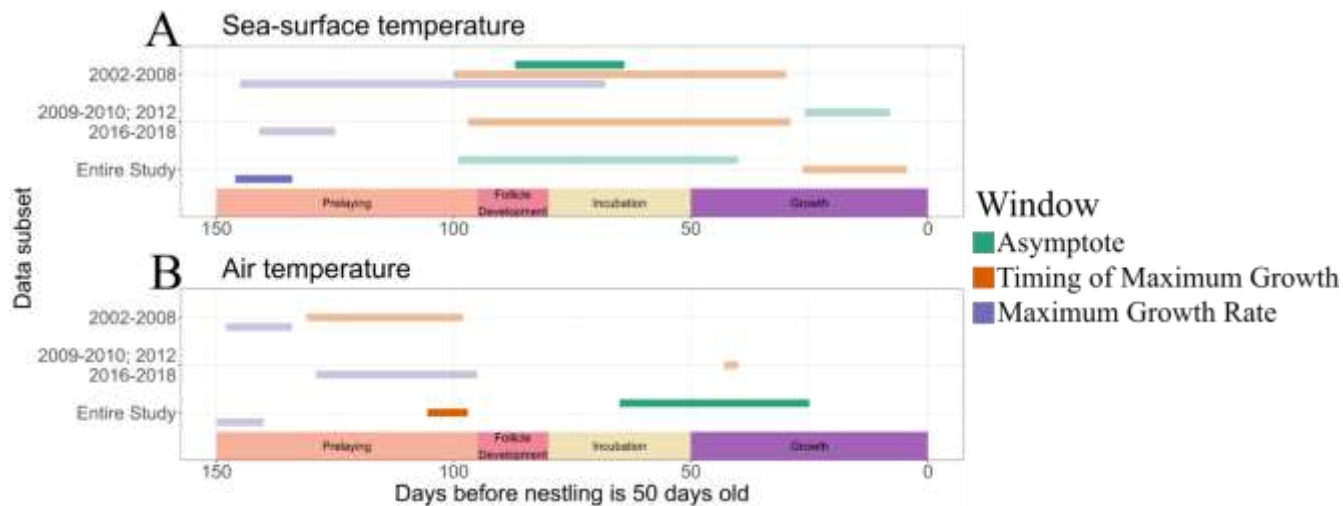
**Figure 4.3: : Model predicted effects of A) maximum air temperature during the breeding season alongside the scatter plots of B) individual asymptotes (g), C) maximum growth rate (g/day), and D) the timing of maximum growth rate of second-hatched kittiwake chicks, across minimum air temperature during the breeding season.**

Individual estimates in scatterplots (B, C, D) are the summed annual and individual group effects estimated in our baseline linear mixed effect model and they do not account for estimate error (see Hadfield et al., 2010; Houslay & Wilson, 2017), therefore the plotted relationships are just for visualization of effects identified in our sliding window analysis. Details of the model are presented in Appendix B-I table B31.



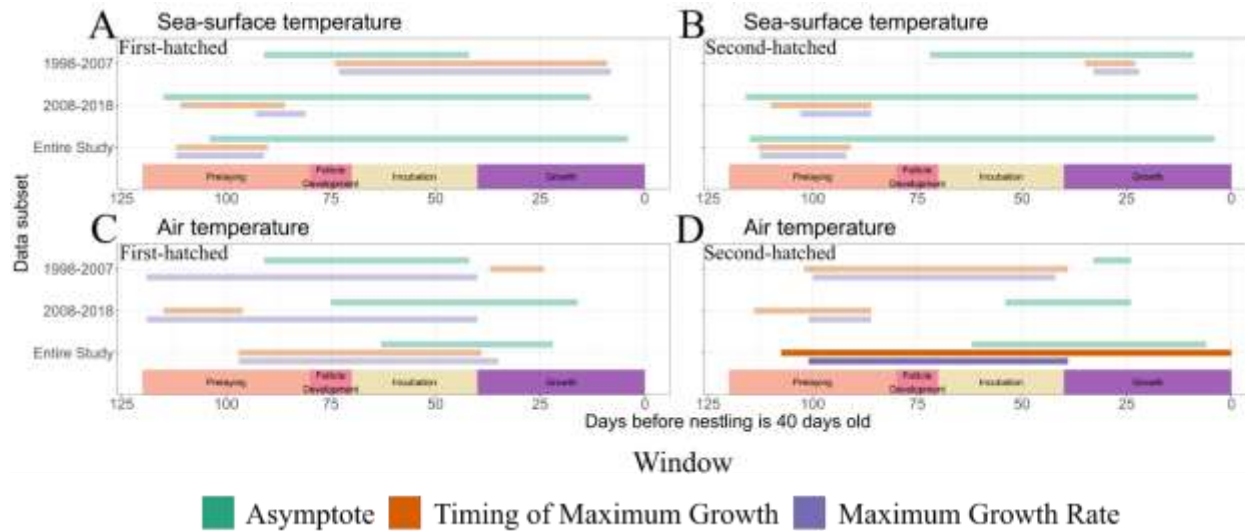
**Figure 4.4: Windows identified in our sliding window analysis as the best predictors of either the intercept or slope of murre growth.**

Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature, air temperature, or percentage ice-cover). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016; van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (1986-1994, top of y-axis), a contemporary period (1995-2010, 2017-2018; middle of y-axis), and the entire study period (1986-2010, 2017-2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predict the intercept of murre growth and the purple bar below indicates the start and end of a window that predicts the slope of murre growth. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are in Appendix B-I tables B23, 24, 25. Details of models for murre split before and after 1999 are in Appendix B-I tables B26, 27.



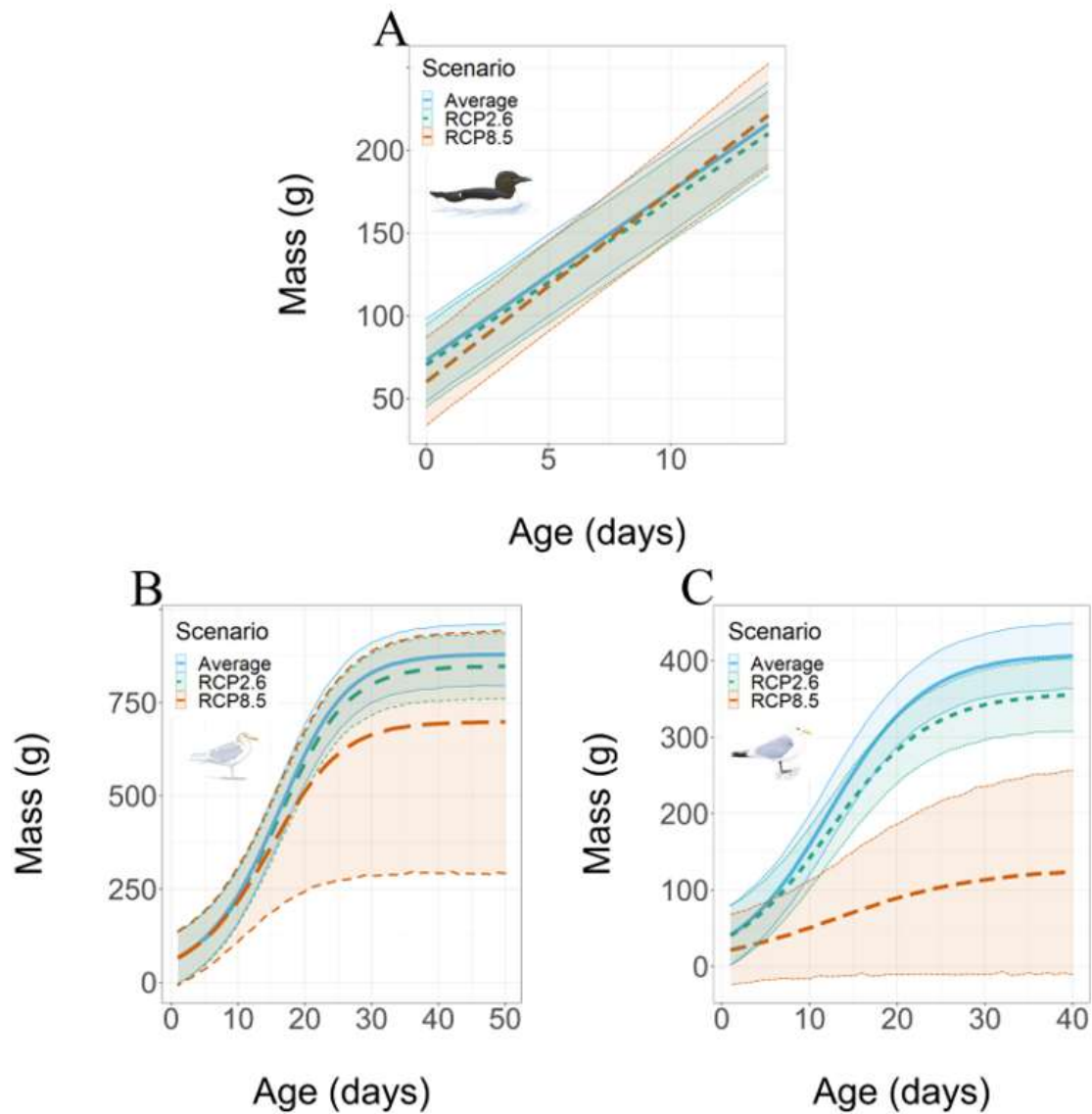
**Figure 4.5: Windows identified in our sliding window analysis as the best predictors of either the asymptote, timing of maximum growth, or maximum growth rate of gull growth.**

Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature or air temperature). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016; van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (2002-2008; top of y-axis), a contemporary period (2009-2010, 2012, 2016-2018; middle of y-axis), and the entire study period (2002-2010, 2012, 2016-2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predict the asymptote of gull growth, the middle yellow bar indicates the median start and end of windows that best predict the timing of maximum growth, and the purple bar below indicates the start and end of a window that predicts the maximum growth rate. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are detailed in Appendix B-I tables B28, 29, 30.



**Figure 4.6: Windows identified in our sliding window analysis as the best predictors of either the asymptote, maximum growth rate, or slope of kittiwake growth.**

Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature or air temperature). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey and Pol 2016; van de Pol et al. 2016). Windows for three data subsets are shown: a historical period (1998-2007; top of y-axis), a contemporary period (2008-2018; middle of y-axis), and the entire study period (1998-2018; bottom of y-axis). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predicts the asymptote of kittiwake growth, the middle yellow bar indicates the median start and end of windows that best predict the timing of maximum growth, and the purple bar below indicates the start and end of a window that predicts the maximum growth rate. Bolded bars were retained in our model selection process and faded bars were not. Details of each model are detailed in Appendix B-I tables B31, 32, 33.



**Figure 4.7: Predicted growth of A) murrelets, B) gulls, and C) second-hatched kittiwakes under average conditions across the study of each species (blue solid line), a low emission climate change scenario (RCP2.6; green short dashed lined), and a high emission climate change scenario (RCP8.5; orange long dashed line).**

Details of models underlying predictions are in Appendix B-I tables B23, 28, 31.

**Table 4.1: Details of the seabird datasets.**

Thick-billed murres lay single egg clutches, and we are unable to reliably disentangle the first, second, and third egg laid in glaucous-winged gull clutches.

Species	Colony location	<i>n</i> years/chicks	Average number of mass measurements per chick	Study years with chick growth data
Thick-billed Murre	Coats Island (Northern Hudson Bay; 62°56'N, 82°0'W)	27/ 1528	6.08	1986-2010; 2017- 2018
Black-legged Kittiwake	Middleton Island (Gulf of Alaska; 59°26'N, 146°20'W)	21/ 1980	First-hatched: 6.88 Second-hatched: 4.5	1998-2018
Glaucous- winged Gull	Middleton Island (Gulf of Alaska)	13 / 1558	2.2	2002-2010; 2012; 2016-2018

**Table 4.2: Bayes  $R^2$  values with associated 95% credible intervals in brackets for models of each period and species-specific growth parameters.**

Bayes  $R^2$  values are calculated from models predicting a growth parameter and all significant environmental windows from our sliding window analysis of growth parameters.

<b>Time Period</b>	<b><math>R^2</math> Value</b>		
<b>Murres</b>	<b>Growth Rate</b>	<b>Average Mass</b>	
Historic	0.07 [0.03, 0.11]	0.14 [0.09, 0.20]	
Contemporary	0.17 [0.14, 0.21]	0.32 [0.28, 0.36]	
Entire	0.07 [0.047, 0.094]	0.25 [0.22, 0.28]	
<b>Gulls</b>	<b>Maximum Growth Rate</b>	<b>Timing of maximum growth rate</b>	<b>Asymptote</b>
Historic	0.18 [0.13, 0.22]	0.25 [0.20, 0.30]	0.07 [0.04, 0.10]
Contemporary	0.07 [0.04, 0.11]	0.07 [0.04, 0.11]	0.05 [0.02, 0.08]
Entire	0.08 [0.06, 0.11]	0.09 [0.06, 0.11]	0.03 [0.02, 0.05]
<b>Alpha Kittiwakes</b>			
Historic	0.54 [0.50, 0.58]	0.37 [0.32, 0.42]	0.05 [0.02, 0.09]
Contemporary	0.46 [0.42, 0.50]	0.25 [0.20, 0.30]	0.24 [0.19, 0.29]
Entire	0.43 [0.40, 0.46]	0.28 [0.24, 0.31]	0.13 [0.10, 0.17]
<b>Beta Kittiwakes</b>			
Historic	0.57 [0.52, 0.61]	0.51 [0.46, 0.56]	0.16 [0.10, 0.22]
Contemporary	0.34 [0.28, 0.39]	0.21 [0.15, 0.27]	0.49 [0.44, 0.53]
Entire	0.40 [0.35, 0.44]	0.30 [0.25, 0.34]	0.38 [0.34, 0.42]

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## Chapter 5

### **The magnitude of selection on growth varies among years and increases under warming conditions in a subarctic seabird**

#### **5.1 Abstract**

Because of ongoing rapid climate change, many ecosystems are becoming both warmer and more variable, and these changes are likely to alter the magnitude and variability of natural selection acting on wild populations. Critically, changes and fluctuations in selection can impact both population demography and evolutionary change. Therefore, predicting the impacts of climate change depends on understanding the magnitude and variation in selection on traits across different life stages and environments. Long-term experiments in wild settings are a great opportunity to determine the impact of environmental conditions on selection. Here we examined variability in the strength of selection on size traits of nestling black-legged kittiwakes (*Rissa tridactyla*) in a 25-year study including a food supplementation experiment on Middleton Island in the Gulf of Alaska. Using mixed effect models, we examined the annual variability of stage-specific and resource-specific selection gradients across 25 years. We found that **1)** larger and heavier hatchlings were the most likely to survive during early ontogeny, **2)** non-food supplemented younger nestlings in a brood experienced the strongest selection, and **3)** warmer conditions increased the magnitude of selection on nestling mass and affected non-food supplemented and second-hatched nestlings the most. Our results suggested that variable resource dynamics likely caused some of the changes in selection from year to year and that warming conditions increased the strength of selection on subarctic seabird growth. However, our experimental manipulation revealed that local environmental heterogeneity could buffer the selection expected from broader climatic changes. Consequently, understanding the interactive

effects of local conditions and general changes in climate seems likely to improve our ability to predict future selection gradients.

## **5.2 Impact summary**

Measuring natural selection in wild populations is necessary to 1) determine which phenotypes result in improved reproduction and survival, 2) determine which individuals are likely to be removed from the population, and 3) make evolutionary predictions. However, climate change is thought to be changing natural selection in a wide variety of environments across the globe. Differences in environmental conditions mean that some populations are likely to experience stronger changes in natural selection than others under climate change. Local differences in natural selection could mean that some populations will be more affected by changes induced by climate change. In this study, we use data from a long-term experimental study of black-legged kittiwakes (*Rissa tridactyla*) to compare strength and variation in natural selection on nestling size traits between experimentally fed nestlings and unfed nestlings, among nestlings at different ages, and between first and second hatched nestlings in a nest. We evaluated 1) whether natural food conditions and later hatching rank increased the strength and variation of selection experienced by nestlings, and 2) whether climatic variation correlated with selection on nestlings. We found that natural selection was strongest early in life and that it was consistent in direction, such that heavier nestlings were more likely to survive to the next age category. Selection was strongest on second-hatched nestlings and nestlings that did not receive food supplementation. Warmer climatic conditions increased the strength of selection on nestling mass, and non-food supplemented and second-hatched nestlings experienced the strongest changes in selection under warmer conditions. Therefore, warming climatic conditions have the potential to change natural selection acting on groups within a population differently. These

findings indicate the importance of considering the interaction among climate change, life-stage, and competition when trying to understand changes in natural selection associated with climate change in wild populations.

### **5.3 Introduction**

A major difficulty in predicting adaptive responses to human-altered environments is accounting for and understanding the drivers of variation in selection. The environment varies across time and space and these fluctuations result in variable selection for wild populations (Endler 1986; Chevin et al. 2015). In theory, fluctuations in selection could impact genetic variation, phenotypic plasticity, and the interplay of evolution and demography (Gavrilets and Scheiner 1993; Bürger 1999; Lande and Shannon 1996; Via and Lande 1985). However, determining the importance of variation in selection depends on empirically documenting patterns of selection in wild populations (Chevin et al. 2015; Gamelon et al. 2018; Le Vaillant et al. 2021).

Environmental heterogeneity could alter how changes in selection driven by climate change impact a population (Garant et al. 2007; Corsini et al. 2021). Under low resource conditions, larger individuals might be better able to persist longer without food and outcompete other individuals for limited food availability, which would translate into increased selection on nestling body mass (Peters 1983; Mock and Parker 1997). Because warmer conditions are expected to decrease food availability in many habitats (e.g. through phenological mismatch or decreased prey abundance) we might expect to see stronger selection for larger individuals in warm conditions.

To predict the changes in selection under climate change, we need to understand how it operates across life-stages and whether selection changes in the same way across life-stages with

changing environmental conditions. Characterizing selection across ontogeny can provide insights into when the direction or strength of selection might change across life stages (Price and Grant 1984). Strong selective events early in life might shape the within-generation distribution of phenotypes resulting in altered survival and reproductive output relative to a population not experiencing early life selection (Bell et al. 2021).

Here we examine the form and strength of selection on size traits in nestling black-legged kittiwakes (*Rissa tridactyla*) across ontogeny, with an experimental comparison between non-food supplemented and food supplemented nestlings. Because selection can act on multiple traits simultaneously (Lande and Arnold 1983), we measured selection gradients for two traits we hypothesized to be important for nestling survival, mass and wing-length. Black-legged kittiwakes are long-lived (life expectancy ~13 years; Hatch et al. 2020) pelagic gulls that breed annually on elevated ledges (e.g. cliff or artificial ledges). Kittiwakes on Middleton Island spend the nonbreeding season at variable distances from the breeding colony along the North-East Pacific and food supplemented birds remain closer to the colony and return earlier (Whelan et al. 2020). Middleton kittiwakes breed in the early spring (April-May) and lay one to three egg clutches. Of all nests with eggs on Middleton Island, one, two, and three egg clutches correspond to ~ 10%, 88%, & 1% of non-food supplemented nests and ~ 4%, 91%, & 5% of food supplemented nests. The majority of nestlings hatch in June and July and fledge in July, August, and early September. Because kittiwakes often share a nest with a sibling, the survival of a nestling can depend on its ability to outcompete its sibling (White et al. 2010; Merklings et al. 2014). Hence the presence and size of a sibling might shape the selection on nestling growth. We addressed three questions: 1) What is the strength and form of selection acting on nestling size traits across ontogeny, food environments, and nestling rank? 2) Does interannual variation in

selection differ among ontogenic stages, food supplementation, and nestling rank? 3) If selection varies in magnitude or direction across years, is it predicted by environmental conditions that we expect to change under climate change? Generally, we expected that larger nestlings would be more likely to survive, and selection would be strongest early in ontogeny and for the second-hatched nestling in a brood. We expected higher variability in selection in non-food supplemented nestlings and higher variability in selection for second-hatched nestlings, as the competition faced by non-food supplemented, and second hatched-nestlings is likely to be more dependent on food conditions (Braun and Hunt 1983; White et al. 2010; Hatch 2013; Sauve et al. 2021). Finally, we expected that warmer sea-surface temperatures would predict years with stronger selection on nestling size. Warmer sea-surface temperatures result in poor foraging conditions for kittiwakes, which is expected to increase sibling competition and potentially amplify the competitive advantage of being large (Braun and Hunt 1983; Gill and Hatch 2002; Hatch 2013; Merklung et al. 2014). Foraging conditions for kittiwakes appear to be impacted by environmental conditions both two years prior to and during the breeding season (Sauve et al. 2021; Whelan et al. 2022). The main prey fishes of kittiwakes take about two years to mature so it is thought that environmental effects two years prior to a breeding season might impact prey availability in any given year (Doyle et al. 2019; Whelan et al. 2022). Here we evaluate both time periods as potential predictors of selection on nestling size traits.

## **5.4 Methods**

### **Black-legged kittiwake colony and food supplementation experiment**

We used 25 years (1996-2021) of data from a colony of black-legged kittiwakes on Middleton Island (Gulf of Alaska; 59°26'N, 146°20'W) where kittiwakes nest on an abandoned radar tower (Gill and Hatch 2002). The tower is a 12-walled polygon where artificial nest sites were created

on the upper storeys, allowing observation through one-way glass windows from inside the tower. Each year, research teams provided a subset of the nesting pairs with capelin *Mallotus villosus* through a polyvinyl chloride tube at their nest site three times a day from May until mid-August (further details in Gill and Hatch 2002). The primary prey of kittiwakes during colder breeding seasons was capelin, but in warm years kittiwakes foraged on a higher proportion of Pacific herring *Clupea pallasii*, invertebrates, myctophids Myctophidae, sable-fish *Anoplopoma fimbria*, salmon *Oncorhynchus* spp. and sand lance *Ammodytes hexapterus* (Hatch 2013). The same nesting sites were studied each year but parental pairs at fed sites changed because of death or competition for sites. Nests were checked twice daily (at 9:00 and 18:00 H) throughout the season to record laying and hatching. Within a brood, eggs hatch an average of 1.64 days apart (Merkling et al. 2014), and so first-hatched and second-hatched nestlings were distinguished with different colours of a nontoxic marker on their head to distinguish nestling rank (first-hatched marked with red & second-hatched marked with blue) until banded at ~5 days of age. Every 5 days from hatching to 40 days (i.e. close to fledging) mass was weighed to the nearest 0.1 g using an electronic scale and wing length (“size”) was measured to the nearest 1mm using a wing ruler. Note that body condition (residuals of body mass regressed on wing length) was highly correlated to body mass (e.g. age 0 correlation = 0.96 [0.95, 0.96] & age 40 correlation = 0.98 [0.97, 0.99]) so we opted to use body mass and wing length in our analysis. Several experiments have been conducted on the nests previously (e.g. Merklng et al. 2014, 2016), so we excluded data from nestlings that were experimentally manipulated (~9.1% of breeding attempts excluded, beyond food supplementation).

#### **5.4.1 Statistical analyses**

Our goal was to examine viability selection on mass and size throughout ontogeny, so our response variable was always survival to the next age class and our predictor(s) were the traits measured at the current age class. We evaluated our different fitness functions (below) for traits measured 9 times throughout the growth period (Ages 0 [hatching day], 5, 10, 15, 20, 25, 30, 35, 40 days). In our fitness functions, we evaluated body mass and wing length as predictors of survival and these traits were standardized within each age class by subtracting the mean trait value and dividing by the standard deviation. Depending on the fitness function, we ran linear or non-linear generalized mixed models. All models of survival were run with a binomial error distribution and ‘logit’ link function using the R package ‘brms’ in R version 4.1.3 (Bürkner 2017; R Core Team 2021). Selection estimates were back transformed to data scale following Janzen and Stern (1998) and de Villemereuil et al. (2020).

#### **5.4.2 Fitness functions**

Following recent work examining fluctuating selection (Chevin et al. 2015; de Villemereuil et al. 2020), we compared different fitness function shapes for each selective period: 1) a flat fitness function where survival is independent of mass or wing length, 2) a straight line where survival probability changes monotonically with mass or wing length, 3) a flat two-dimensional surface where survival changes monotonically as a function of mass *and* wing length, 4) a Gaussian fitness function where survival probability is optimized at some value of mass or wing length, and 5) a bivariate Gaussian landscape where survival probability is optimized as a function of mass *and* wing length. See the Appendix C for the function equations. We used a leave-one-out information criterion (LOOIC) derived from approximate cross-validation using Pareto-smoothed importance sampling (PSIS) to compare and evaluate the predictive performance of each fitness function (Vehtari et al., 2017). The lowest LOOIC value was considered the best

model and any model within 5 LOOIC values of the best LOOIC model was considered as a top model. For each of our fitness functions, we estimated the parameters of each function at each food treatment and hatching order grouping using fixed effects. Additionally, because differences among ages in standardized selection gradients could be due to the measurement of selection at different points along a single non-linear selection function acting on mass independent of age (e.g. Hunter et al. 2018), we estimated linear selection gradients on absolute non-standardized mass and wing length for each age category (fitness function 3 above). Differences among age-specific selection gradients measured for absolute mass and wing-length will indicate whether our selection functions are indeed varying among age classes or are the result of our age categories sampling different segments of the same fitness function. While the above functions link theoretical models of selection with our empirical data, we also wanted to examine a less constrained shape for the viability fitness function. So, we also modelled survival as a smooth function of standardized age specific mass and wing length using a general additive model (GAM) and the default regression spline basis. We compared these GAM models to the fitness functions described above to detect potentially unexpected patterns that would go unnoticed in the above mentioned models.

#### **5.4.3 Variability of selection**

For each selective episode, if our evaluation of fitness functions indicated that the monotonic or optimum fitness models best predicted survival, we allowed the fitness function to vary annually. Because we aimed to determine if different treatments or nestling ranks affected the variability of selection, we estimated the annual variance in our fitness function parameters for each experimental and rank grouping. If our best model of selection was a line or plane (fitness function shapes 2 & 3) we allowed the slope(s) to vary among years and if our best model of

selection was an optimum function (shapes 4 & 5) we allowed the optimum(s) and maximum fitness parameters to vary among years. We did not allow the width of our optimal fitness functions to vary among years because our sample sizes were unlikely to provide sufficient power to estimate fluctuations in the fitness function width (de Villemereuil et al. 2020). We first allowed our selection function to vary among years for all nestling rank and treatment groups (synchronous annual variation in selection among treatment & rank groups) and then allowed our selection function to vary differently for each nestling rank and treatment group (heterogenous variation in selection among treatment & rank groups). We compared these two parameterizations using LOOIC to determine support for synchronous or heterogenous variability of selection among rank and treatment groups (Vehtari et al. 2017).

#### **5.4.4 Environmental correlates of selection**

If our top model indicated that selection varied among years, we evaluated whether selection parameters correlated with four environmental variables: Pacific Decadal Oscillation (PDO) during the breeding season; minimum air temperature during the breeding season; average sea surface temperature during the breeding season (previously shown to correlate with nestling growth parameters and annual fecundity in the population; Hatch 2013; Sauve et al. 2022); and PDO two-years prior to breeding (previously shown to predict the laying date of kittiwakes at Middleton; Whelan et al. 2022). We ran eight models and compared their LOOIC values to each other and to our top model of variation in selection without an environmental effect. Each model only contained one of the environmental variables described above, and for each environmental variable, we ran two models: one with the environmental variable as a fixed effect that impacts selection on all kittiwake ranks and treatments in the same way (no interaction between variable and our rank & treatment groups); and one with the environmental variable as a fixed effect that

impacts selection parameters differently depending on a nestling's rank and treatment (an interaction between environmental variable, nestling rank, and treatment).

## **5.5 Results**

### **5.5.1 Overall patterns of selection**

In all food treatment and nestling rank groups, the highest nestling death counts occurred in the first 20 days after hatching, and deaths were most common in the non-food supplemented nestlings (Fig. 5.1; Table 5.1). Heavier nestlings were more likely to survive to the next age class (Fig. 5.2A) and wing length did not predict survival throughout the nestling period (Fig. 5.2B). Selection gradients for mass were strongest during early ontogeny for non-food supplemented compared to food supplemented nestlings (Fig. 5.2A), and for second-hatched compared to first-hatched nestlings. However, differences in selection among groups disappeared as nestlings aged, and did not exist for selection gradients on wing length (Fig. 5.2B). Selection gradients measured for absolute mass also indicated selection was the strongest during early ontogeny, but indicated a more rapid drop off in selection strength with age (Appendix C Fig. C1). The top fitness function for each selective period always included mass, but during early ontogeny our top fitness function tended to include wing length (ages 0, 10, and 15, but not 5; Appendix C Fig. C2; Appendix C Tables C1 – 9; Appendix C). Our best (lowest LOOIC) fitness function of compared functions at hatching was a bivariate Gaussian function of mass and wing length, while the best functions at 10 and 15 days of age were flat planar functions of mass and wing length (Appendix C Fig. C2). The best fitness functions at every other age (5, 20, 25, 30, 35, & 40) were linear functions of age-specific masses (Appendix C Fig. C2). GAMs indicated that in most cases survival probability plateaued as mass increased, but with larger uncertainty in survival probability at the heaviest masses at age 0, 5, & 40 (Appendix C Fig. C3). GAMs

indicated generally flat fitness functions for wing length, but with large uncertainties of survival probability at short and long wing lengths (Appendix C Fig. C4).

### **5.5.2 Variability of selection**

All age-specific fitness functions that allowed annual variation in selection functions outperformed models with constant selection across years (Appendix C Tables C1-9), except the fitness function at age 30. In almost all cases, half of the top selection models allowed the fitness function parameters to vary synchronously among years and half allowed fitness function parameters to vary differently among years for all hatching rank and food supplementation groups (Appendix C Tables V1-9).

### **5.5.3 Environmental correlates of selection**

The only selective periods when models of survival were improved by the addition of environmental predictors were at ages 0 and 15 days. During all other selective periods, a model without any environmental effects that only included annual fluctuations in the fitness function was the best or a top model ( $\Delta\text{LOOIC} = 0$  or  $\Delta\text{LOOIC} < 5$ ; Appendix C Tables C20-28). During the selective periods when an environmental predictor improved the fitness function (ages 0 and 15) the lowest air temperature during the breeding season was the environmental predictor of selection parameters. We identified two top models for survival from age 0 to 5 that both suggested the lowest air temperature during the breeding season affected selection parameters, but one model suggested air temperature increased the optimal mass for all groups and the other suggested air temperature altered fitness function parameters differently for each nestling rank and treatment (Appendix C Table C29; Fig. 5.3). The best and only top model for survival from age 15 to 20 suggested stronger selection on mass under warmer air temperature conditions (Appendix C Table C32). Additionally, for both selective periods (age 0 to 5 & age 15 to 20)

survival was slightly higher for nestlings with shorter wing lengths under warmer conditions (Appendix C Tables C29 & 32).

## **5.6 Discussion**

Based on patterns of nestling survival in a long-term experimental study of black-legged kittiwakes, we found that 1) selection on nestling mass weakened with time after hatching and selection on mass in an average year was strongest for second-hatched and non-food supplemented nestlings, 2) inter-annual variation in the magnitude of selection was ubiquitous across the nestling growth period, and 3) when selection was strongest (the first 20 days after hatching) warmer conditions selected for heavier nestlings with shorter wings and colder conditions weakened the magnitude of selection.

### **5.6.1 Selection on mass**

Like many investigations of phenotypic selection on size traits we found evidence of selection favouring heavier individuals (Kingsolver and Diamond 2011; Hajduk et al. 2020). Kittiwakes exhibit facultative siblicide and larger nestlings might be better able to survive aggression from siblings (Braun and Hunt 1983). Increased mass could also be advantageous because of an increased tolerance to stressful thermal environments or an ability to persist when food is scarce (Peters 1983, p 67 – 78; Hone & Benton 2005). Whether the consistent (in direction) selection observed for all groups leads to evolutionary change in mass of nestlings will depend on whether there is an additive genetic covariation between nestling mass and survival or reproduction (Price et al. 1988; e.g. Hajduk et al. 2020). Evolutionary change will also depend on trade-offs between parental fitness and nestling traits (Willham 1972). Understanding the evolution of nestling traits depends on understanding the drivers of fitness in parents and offspring and here we provide a detailed investigation of selection on offspring (Hadfield 2008; Thomson et al. 2017).

We examined the early developmental stage of a generally long-lived seabird and found decreasing selection gradients with age. Like our study, investigations of blue tits (*Cyanistes caeruleus*) and southern elephant seals (*Mirounga leonine*), also found stronger selection for mass during early ontogeny versus late ontogeny (Thomson et al. 2017; Oosthuizen et al. 2018). These empirical results follow expectations with senescence theory that traits expressed early in life will have a greater impact on fitness than traits expressed late in life (Williams 1957). However, in some taxa (e.g. many plants) age might not be a good predictor of developmental stage. In these cases, selection strength and age could covary positively within a developmental stage (e.g. Caswell and Salguero-Gómez 2013; Roper et al. 2021).

Because selection is often estimated for traits that are only expressed or measured later in life, total selection for body mass may frequently be underestimated. As some individuals do not survive to express traits later in life, selection measured at later stages does not account for selection against phenotypes that are counter-selected early in life (Hadfield et al. 2008). Depending on the phenotypic and additive genetic (co)variance of mass across early and late age classes, the distribution of phenotypes and breeding values for mass in adult birds could be shaped by early life selection in addition to the commonly documented selection for heavier masses during adult stages (Hadfield 2013; Thomson et al. 2017; Gomulkiewicz et al. 2018). While we still need information on the additive genetic covariance of mass, wing length, and survival to make predictions of evolutionary change, measurements of phenotypic selection indicate that 1) any plastic mechanisms that result in heavier nestlings (at early life stages and under all our explored environmental conditions) are adaptive in terms of offspring viability and 2) the within generation change of phenotypes are shaped such that relatively heavier individuals outcompete lighter individuals early in life. Whether these within generation changes in

phenotypes affect survival and reproductive output at later life stages warrants investigation (e.g. Bell et al 2021).

### **5.6.2 Variation in the magnitude of selection**

We found evidence for annual variation in selection across each growth episode. To date, studies of fluctuating selection have focused on phenological traits, and our study agrees with previously described patterns of selection on phenology in birds and mammals that suggest that selection tends to vary among years in magnitude but not direction (de Villemereuil et al. 2020).

While we predicted among-year variation in selection to be greater for non-food supplemented and second hatched nestlings, we did not detect differences in variability of selection among groups. We did however identify large confidence intervals for estimates of selection on mass in non-food supplemented and second-hatched nestlings (Fig. 5.2). Large confidence intervals in selection parameters could suggest that selection on mass of second-hatched nestlings depends greatly on within breeding season variation. A recent study of snapdragons (*Antirrhinum majus* L.) indicates that natural selection can vary at very small spatial scales and broadly many investigations of adaptive phenotypic and genetic differences suggest that selection must sometimes vary at fine spatial scales (Marrot et al. 2022; Richardson et al. 2014). The microclimates of the radar tower on Middleton Island can vary greatly and selection could vary even across small spatial scales (Lacey 2018). Further, we demonstrated that differences in resource environments experienced by nestlings might alter the strength of selection on mass (Fig. 5.2). Therefore, any differences in resource environment because of parental traits like phenology or care are also potential causes of variation in selection experienced by second-hatched non-food supplemented nestlings (Sauve et al. 2021).

### **5.6.3 Environmental predictors of selection and implications for climate change**

We evaluated several environmental variables as possible predictors of fitness function parameters. Lagged PDO, which influences breeding phenology, does not also predict the selective environment that nestlings will face. Instead, warmer minimum air temperature during a breeding season is associated with stronger positive selection on mass at earlier ages (Sauve et al. 2021). Interestingly, this variable was associated with slower growth and smaller sizes at fledging. An association between warmer air temperatures and smaller nestlings could suggest that nestlings might be plastically adjusting to a smaller size under the same conditions that select for larger nestlings (i.e. a maladaptive plastic response).

Warmer conditions seem likely to increase the strength of selection on mass and, possibly, wing length. This association between mass and survival contrasts with some predictions that climate change will favour smaller body size (Millien et al. 2006; Teplitsky and Millien 2014). But, the hypothesized mechanism driving selection for smaller body sizes is expected to arise from improved heat tolerance associated with small size (Salewski and Watt 2017). We think that the main mechanism of selection acting here is competition among siblings, and kittiwake nestlings seem unlikely to be thermally challenged regularly as air temperatures do not exceed thermal neutral temperatures of 33 to 35°C (Bech et al. 1984). We hypothesize that in years of poor foraging conditions, heavier nestlings will be better able to survive periods of low food availability and increased aggression from siblings and neighbours (Hone & Benton 2005). Across many taxa, heavier individuals are able to survive periods of scarcity and in many avian species, especially those with asynchronous hatching, sibling competition is thought to increase under poor food conditions (Peters 1983; Mock and Parker 1997). Starvation itself may modulate increased aggression in nestlings, or parents may adjust food allocation or egg hormones affecting behavioural interactions in the nest (Groothuis et al. 2005; Shizuka & Lyon 2013). Our

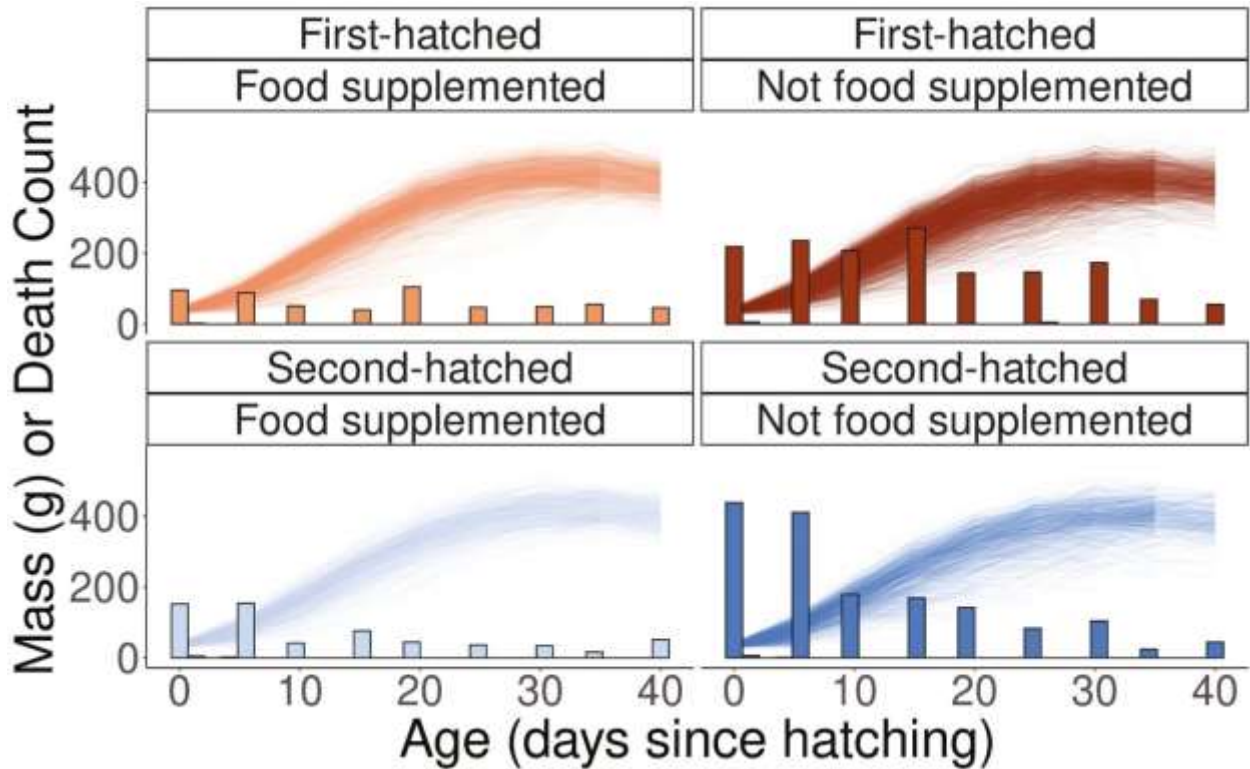
results suggest that in species with environmentally modulated sibling competition, food supplementation (e.g. bird feeders or human garbage) could affect rates of adaptation to warming climatic conditions.

#### **5.6.4 Conclusions**

We conclude that selection for heavier black-legged kittiwakes during early ontogeny was constant in direction but increased in magnitude under warmer conditions. We confirm that in black-legged kittiwakes early ontogeny is a period of strong selection and that this could be true for other long-lived species that experience variable environmental conditions. The specific changes in strength of selection we detected were affected by the food and sibling environment a nestling experienced. Future research will further decompose the variation in nestling mass and survival into genetic, and environmental components to determine if evolutionary change is expected under warming conditions. Further, the implications of a within generation change towards larger masses should be investigated, and plastic responses in mass should be quantified to determine whether they are adaptive or not.

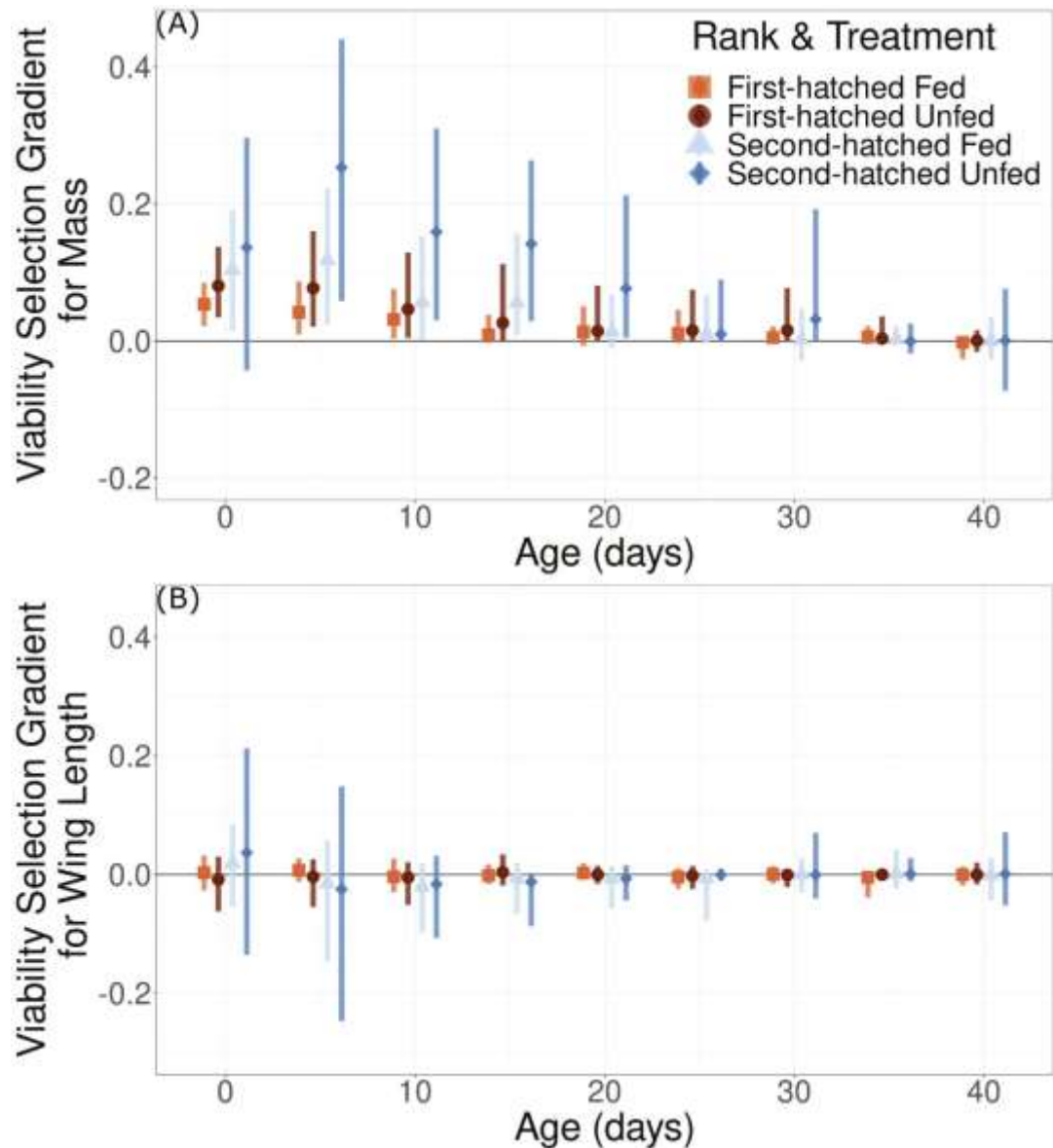
**Table 5.1: Sample sizes of nestlings at each age class by hatching order and food treatment with trait measurements.**

<b>Age</b>	<b>Non-food supplemented</b>		<b>Food supplemented</b>	
	<b>First-hatched</b>	<b>Second-hatched</b>	<b>First-hatched</b>	<b>Second-hatched</b>
<b>0</b>	1923	1200	1098	738
<b>5</b>	1728	786	1004	575
<b>10</b>	1539	573	954	511
<b>15</b>	1511	531	964	505
<b>20</b>	1416	480	950	490
<b>25</b>	1461	463	910	463
<b>30</b>	1270	422	878	458
<b>35</b>	1176	391	849	439
<b>40</b>	671	439	668	224



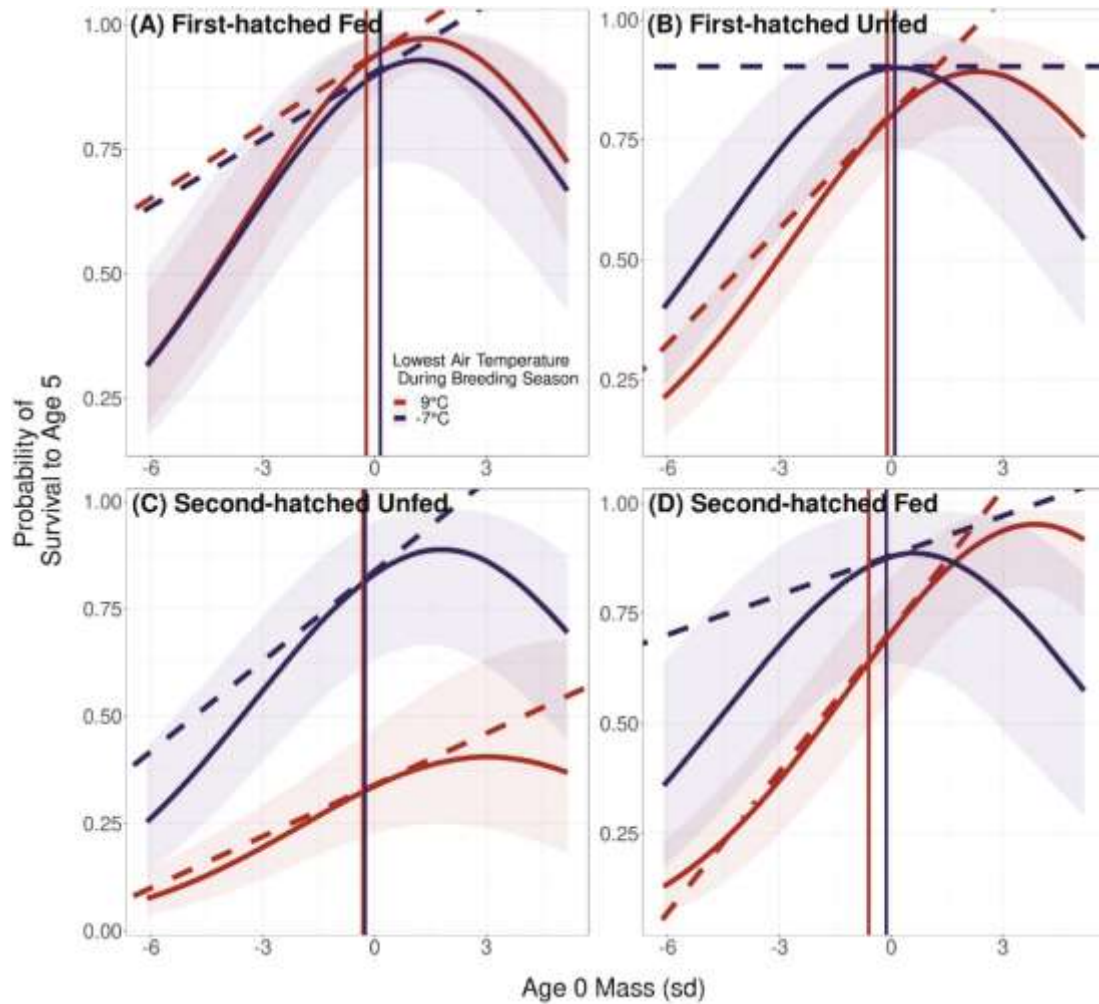
**Figure 5.1** Death counts and individual nestling mass measurements at each age step considered in this study.

Bars indicate the number of nestlings that died between one mass measurement and the next. There is only one y-axis because the left y-axis is either the mass of individuals in grams or the count of individuals that did not survive to the next measurement age. Thin coloured lines indicate the mass measurements taken for each age and each individual. Bars and lines are coloured and grouped by nestling rank and food treatment groups. Brown colours indicate first-hatched nestlings, and blue colours indicate second hatched nestlings. Lighter colours indicate food supplemented nestlings while darker colours indicate non-food supplemented nestlings.



**Figure 5.2 Viability selection gradients for A) mass and B) wing length.**

Selection gradients are transformed from logistic regression to the data scale following Janzen and Stern 1998 and Villemereuil et al. 2020. Points and 95% confidence intervals are coloured and grouped by nestling rank and food treatment groups. Brown colours indicate first-hatched nestlings and blue colours indicate second hatched nestlings. Lighter colours indicate food supplemented nestlings while darker colours indicate non-food supplemented nestlings.



**Figure 5.3: The association between the minimum air temperature during a breeding season and the fitness function from Age 0 to Age 5 with heterogenous effects on each nestling rank and food treatment group.**

For first-hatched food supplemented (A), first-hatched non-food supplemented (B), first-hatched non-food supplemented (C), and second-hatched non-food supplemented (D) the conditional (holding wing-length constant) Gaussian fitness function of mass is displayed under the warmest minimum air temperature during the breeding season (9°C; red) and minimum air temperature during the breeding season (-7°C; dark blue). Solid curves lines indicate the gaussian fitness function with associated 95% confidence intervals, while solid vertical lines indicate the average mass of each nestling group under warm or cold conditionals. Diagonal or horizontal dashed lines indicate the selection operating each nestling group under each temperature condition.

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## **Chapter 6 Exploring the influence of food supplementation on phenotypic variance components of early life traits of black-legged kittiwakes**

### **6.1 Abstract**

Variation underlies nearly all processes in evolution and ecology. To accurately predict the impact of environmental changes on the evolution and ecology of a species or population, we must understand how changes in the environment will affect phenotypic variation. However, we do not know how genetic and environmental contributors to phenotypic variance are expected to change for many traits in a world altered by human activity. Experimental manipulations of individuals in the wild provide valuable opportunities to determine how changes in environmental conditions affect the amount of phenotypic variation in a population. In this study, we combined data from a unique long-term feeding experiment on black-legged kittiwakes *Rissa tridactyla* with pedigree data, to examine the impact of food supplementation on components of phenotypic variation of nestling morphology. Our findings reveal that food supplementation decreased variation from annual environmental conditions; had a limited impact on maternal and paternal contributions to offspring variation; and decreased evolvability of nestling mass and wing length near fledging. While these results suggest that food supplementation may affect demography and reduce rates of evolutionary change, two critical challenges for future research will be to determine whether more variable offspring traits result in heterogeneity among adults in fitness-related traits and to better understand which features or axes of environmental variation are likely to have a generalizable impact on genetic variation. Overall, this study highlights the importance of considering the impact of environmental changes on phenotypic variation in both evolutionary and ecological contexts.

## 6.2 Introduction

Any given population is composed of phenotypically diverse individuals. To make predictions regarding evolutionary and ecological changes in rapidly changing environments (e.g. due to climate change, urbanization, and range shifts), we need to measure this variation and determine whether certain features of the environment have generalizable impacts on components of phenotypic variation (Hoffmann and Sgrò 2011; Thompson et al. 2022). The amount of intra-specific diversity and the relative contribution of genetic and environmental effects to observed phenotypic variation can impact both ecological dynamics, including intra- and interspecific interactions and demography, as well as evolutionary dynamics (Darwin 1859; Bolnick et al. 2011; Cressler et al. 2017). For example, diet specialization among individuals can affect the niche width of a population, and the genetic diversity within a population can affect its adaptive potential (Lynch and Walsh 1998; Bolnick et al. 2003). Importantly, the environment can play a significant role in driving rapid changes in phenotypic variation ascribed to genetic and environmental variation (de Jong 1999; West-Eberhard 2003; Sultan 2015; Wood and Brodie 2015; Capilla-Lasheras et al. 2022). Studying the drivers of phenotypic variation in early life is important because differences early in life are known to contribute to variation among adult phenotypes. Furthermore, selection is known to vary across life stages and is potentially very strong during early life (Price and Grant 1984; Vindenes and Langangen 2015; English et al. 2016; Bourret et al. 2017; Fay et al. 2018).

How genetic variation, especially additive genetic variation ( $V_A$ ), changes as the environment changes is of prime interest when modelling microevolution because selection on the genetic part of a trait leads to adaptive genetic change between generations (Falconer and Mackay 1996). Currently, findings on how additive genetic variation changes from unfavourable to favourable conditions are mixed, and conclusions can differ depending on the conditions

where traits were measured (wild, domestic or laboratory). Many early meta-analyses derived conclusions about changes in genetic variation based on heritability and not on additive genetic variance or evolvability, so it is still unclear exactly how we might expect additive genetic variance to change in response to a changing environment (Hoffmann and Merilä 1999; Hoffmann and Parsons 1997). Laboratory studies of traits under extreme stress revealed higher heritabilities of morphological and life-history traits in extreme environments, but studies of populations of wild birds and other organisms (non-domestic & non-laboratory) have identified increases in the heritability of morphological traits in more favourable conditions (Hoffmann and Merilä 1999; Merilä and Sheldon 2001; Charmantier and Garant 2005). A more recent meta-analysis investigated changes in both heritability and additive genetic variance standardized by the squared mean of the trait (evolvability; Houle 1992) in a range of taxa across field and laboratory studies. While this meta-analysis showed weak trends in heritability across stressful *versus* benign conditions, evolvability and additive genetic variance increased under stressful conditions for life-history traits. At the same time, there was no clear pattern for morphological traits (Rowiński and Rogell 2017).

Current empirical studies provide mixed results, and more studies are needed to determine whether and how we can generalize across traits, taxa, and environments. Phenotypic variation is influenced by many factors in addition to additive genetic variance, most notably environmental variability and parental effects. Broadly, the environmental variation that individuals experience during development could contribute to phenotypic variability in the adult population (Beckerman et al. 2002). Many human-induced environmental changes such as climate change are expected to increase environmental variability (Intergovernmental Panel on Climate Change 2018). Increased seasonal variation might increase phenotypic variation.

Heterogeneity in resources, even within a population, could mean that some micro-habitats produce more variable phenotypes (i.e. individuals within these local environments are more exposed to variable conditions). Cohort effects caused by different early-life environments have the potential to impact offspring variation that could later manifest as differences among adults or cohorts in vital rates (Beckerman et al. 2002). Variation in vital rates among adults in turn can have a broad range of impacts on population dynamics (de Valpine et al. 2014; Vindenes and Langangen 2015).

Another important contribution to offspring trait variance is differences among parents in a population. Effects on offspring from parents will be altered both by local cues during breeding and by the environment(s) that parents experience (Burton et al. 2013; Burton and Metcalfe 2014; Plaistow et al. 2015). Parental contributions to an offspring trait can have their own environmental and genetic components, and increased variation in parental investment could alter the evolutionary potential of an offspring trait (Mcadam et al. 2002; Evans et al. 2018, 2020). However, it is unclear how an unfavourable environment will impact the variation among parents in their contributions to an offspring trait. Certainly, the same processes that impact environmental and genetic variation of offspring could impact variation among parents in investment as a trait, but syntheses on maternal variance have not identified a consistent impact of stressful or unfavourable conditions on maternal variance (Rowiński and Rogell 2017).

To evaluate how components of early-life phenotypic variance change under different environmental conditions in a subarctic seabird, we used morphological data from a long-term (25-year) experimental study of black-legged kittiwakes (*Rissa tridactyla*). A portion of the kittiwakes on Middleton Island are food supplemented (hereafter “fed; versus non-food supplemented “unfed”; Gill and Hatch 2002). We used this long-term data set to test whether

additive genetic, annual, maternal, & paternal variance differed among food supplementation and nestling rank contexts for nestling mass (g) and wing length (mm). Generally, we expected higher additive genetic variance & evolvability for food supplemented nestlings because “favourable” conditions are thought to lead to increased additive genetic variance and heritability of morphological trait compared to “unfavourable” conditions (Charmantier, Kruuk, and Lambrechts 2004; Merilä 1997; Gebhardt-Henrich and Van Noordwijk 1994; Merilä and Fry 1998). We expected higher among-year variation in unfed nestlings because these nestlings are the most exposed to annual variation in food resources. We examined whether these differences existed across offspring ontogeny both because differences in variation might only express themselves later in ontogeny, and because selection during particular stages might have affected the amount of additive genetic variation present. In particular, we showed previously that selection on mass is strongest during early ontogeny in kittiwakes so we might expect less additive genetic variation for morphological traits during this period (Sauve et al. 2023)

## **6.3 Methods**

### **6.3.1 Data collection**

Data were collected from a wild population of black-legged kittiwakes breeding on an abandoned radar tower on Middleton Island, Gulf of Alaska (59°26'N, 146°20'W). Nest sites are observed through one-way glass windows from the inside of the tower. Each year since 1998, research teams provided a subset of the nesting pairs with capelin *Mallotus villosus* through a polyvinyl chloride tube at their nest site three times a day from May until mid-August (further details in Gill and Hatch 2002). The same nesting sites were studied each year but parental pairs at fed sites changed because of death or competition for sites. Nests were checked twice daily (at 9:00 and 18:00 H) throughout the season to record laying and hatching. Females usually lay two

eggs per brood. Within a brood, eggs hatch an average of 1.64 days apart (Merkling et al. 2014), and so first-hatched and second-hatched nestlings were distinguished with different colours of a nontoxic marker on their head (red and blue respectively) until banded at ~5 days of age. Every 5 days from hatching to 40 days (i.e. close to fledging) mass was weighed to the nearest 0.1 g using an electronic scale, and wing length was measured to the nearest 1mm using a wing ruler. Several experiments have been conducted on the nests previously (e.g. Merkling et al. 2014, 2016), so we excluded data from nestlings that were experimentally manipulated (~9.1% of breeding attempts excluded, beyond food supplementation).

### **6.3.2 Pedigree construction**

We constructed a social pedigree by matching the parents breeding at a nest site in a given year with the nestlings hatched at the same site and year. The social pedigree should be a good approximation of the genetic pedigree in this species because black-legged kittiwakes exhibit very low rates of extra-pair copulation & extra-pair paternity (2 out of 313 copulations from 82 pairs; 0 out of 119 offspring from 86 broods; Helfenstein et al. 2004). Behavioural observations of copulations, courtship feeding, and begging behaviour were used to identify the sex of parents each year (Whelan et al. 2022). The pedigree encompassed four generations of kittiwakes, and contained 7082 records with 4903 maternities, 4905 paternities, and 10,876 full siblings.

### **6.3.3 Quantitative genetic analyses**

We used age-specific univariate linear models of mass and wing length to decompose phenotypic variance in mass and wing length into variance components. Univariate linear mixed models were solved using Restricted Maximum Likelihood (REML) and implemented in ASREML-R version 3.6 (Butler et al. 2009). All models included fixed effects of a nestling's rank (first-hatched or second-hatched) and food treatment (food supplemented or non-food supplemented).

We decomposed the variance in mass and wing length into maternal, paternal, annual (cohort), and additive genetic variance. Relatedness matrices derived from the population pedigree were used to estimate additive genetic variance (Kruuk 2004; Wilson et al. 2010; Wolak and Keller 2014).

For each model of age-specific mass and wing length, we started with maternal, paternal, annual, and additive genetic random effects and we used AICc values to determine whether heterogenous variance structure improved model fit based on AICc (Burnham and Anderson 1998; Barton and Barton 2015). For each random effect, we determined whether allowing the variance to differ between food treatments improved model fit. We started by fitting four models with heterogenous variances (1 model with each heterogenous variance grouping at each of our chosen random effects). Whichever model resulted in the lowest AICc value was chosen as the next baseline model, and heterogenous variance structures were added to the remaining random effects and compared to the new baseline model in the next round of comparison. This process was continued until either the addition of random effects no longer improved model fit or all of our random effects had heterogenous variances. A model with an AICc value  $<2$  compared to the base or previous best model was considered an improvement in the model (Burnham and Anderson 1998). We calculated evolvability of mass or wing length as the additive genetic variance of a treatment group divided by the squared mean of mass or wing length of the treatment group. Evolvability is interpreted as the percent trait change expected given that a standardized unit of selection is applied to the trait (Hansen et al. 2011; Houle 1992).

## **6.4 Results**

Food supplemented nestlings and non-food supplemented nestlings were always the heaviest with the longest wings, and the lightest with shortest wings respectively at all age categories

(Tables 6.1, 6.2). First-hatched non-food supplemented nestlings were heavier than second-hatched food supplemented nestlings until 15 days of age and had longer wings than second-hatched food supplemented nestlings until 30 days of age (Tables 6.1, 6.2). Non-food supplemented nestlings had higher phenotypic variance for mass from ages 15 days to 40 days (Fig. 6.1A) and for wing length from 25 to 40 days (Fig. 6.1B).

Mass and wing-length exhibited additive genetic variance, maternal variance, paternal variance, and annual variance at most ages, ranks, and treatment categories (Figs., 6.2, 6.3). Additive genetic variance did not differ clearly between food treatments for most age categories (Figs. 6.2, 6.3). Heterogeneities in additive genetic variance among food treatments and lower average masses and wing lengths in non-food supplemented nestlings resulted in higher evolvabilities for non-food supplemented than food supplemented nestlings from 30 to 40 days of age (Fig. 6.4).

Among year variance in mass was greater in non-food supplemented nestlings from age 0 to 35 days (Fig. 6.2), and among year variance in wing length was greater in non-food supplemented nestlings from age 10 to 40 days (Fig. 6.3). Maternal and paternal variance tended to comprise a small proportion of the total phenotypic variance (~5-20%; Fig. 6.2, 6.3) and maternal and paternal variance components did not differ among treatments for mass or wing length (Figs. 6.2, 6.3). However, among-mother variation in nestling mass was higher (~40%) for age 0 nestling mass (but not wing length) and declined as nestlings aged (Fig. 6.2).

## **6.5 Discussion**

We found evidence that experimental food supplementation can not only improve nestling growth, but also affect the amount of environmental variation in nestling morphological traits, and even the evolvability of these traits. Increased phenotypic variation in some environments

suggests a potentially broader range of ecological interactions and life-history strategies produced in non-food supplemented environments. The increased evolvabilities for traits in non-food supplemented broods suggests increased evolutionary potential for these traits.

Interestingly, these differences in variance components among treatments were only apparent at some ages during nestling growth.

### **6.5.1 Environmental impacts on additive genetic variation**

Based on previous findings that  $V_A$  often increases in more favourable environments (Gebhardt-Henrich and Van Noordwijk 1994; Charmantier and Garant 2005), we predicted lower additive genetic variation in our non-food supplemented kittiwakes. However, we found the opposite result in that whenever we had differences in additive genetic variance between treatments, we had the highest heritabilities, additive genetic variances, and evolvabilities in mass and wing traits in “unfavourable” conditions. For instance,  $V_A$  and evolvability of nestling body mass was higher in unfed nestlings for ages 20 to 40 days old (Fig. 6.4). Notably, other studies have found the opposite pattern for morphological traits (Charmantier and Garant 2005). For example, morphological traits (tarsus length, mass, plant height) have been observed to have higher additive genetic variance following resource supplementation in Eurasian magpies *Pica pica*, burying beetles *Nicrophorus pustulatus*, and field mustard *Brassica rapa* (Rauter and Moore 2002; De Neve et al. 2004; So et al. 2022). Such diversity in results from comparable experiments suggests that the observed decrease in additive genetic variation under resource supplementation is not a general rule.

Many hypotheses have been proposed in line with predictions of higher additive genetic variation in more stressful conditions. These hypotheses range from higher mutation rates under stressful conditions to the breakdown of canalization of phenotypes resulting in increased

variance (Hoffmann and Parsons 1997; Rutherford 2000; Siegal and Bergman 2002; Schlichting 2008). Non-food supplemented nestlings likely experience an increased variety of environmental conditions, and this could result in more genetic differences being expressed because of the increased potential for multiple genotype-by-environment interactions. In some environments, different genotypes might have similar effects, while in another, the different genotypes produce different effects. In this case more “cryptic” genetic diversity can be revealed because the expression of genetic differences only occurs in certain environmental contexts (McGuigan and Sgrò 2009; Paaby and Rockman 2014).

Another potentially interesting explanation for lower additive genetic variation in the high resource environment is that individuals on average tend to be better adapted to the high resource environment (Van Tienderen 1991; Holt and Gaines 1992). This idea is phrased nicely by (Hadfield and Reed 2022, pp. 184) in reference to breeding date: “... birds in high nutrition territories generate more offspring, which means that on average individuals are better adapted to high nutrition environments simply because more genes have come from, and have been subject to selection in, high nutrition environments”. Studies of recruitment on Middleton Island even suggest that the per nest recruitment from food supplemented environments is higher because of the increased fledging success (Vincenzi et al. 2015), and we know that in years with increased food abundance, nestlings from non-food supplemented nests have survival rates comparable to the nestlings from the food supplemented nests (Hatch 2013).

### **6.5.2 Evolutionary responses: evolvability and maternal effects**

Higher additive genetic variances and evolvabilities in non-food supplemented environments indicate a higher evolutionary potential in low-nutrition environments (Fig 6.4). This insight is relevant to many situations in anthropogenic contexts because intentional or unintentional food

supplementation is a common interaction that humans have with wild populations (Murray et al. 2016). Our evolvability estimates are generally low, but at the most extreme indicate almost double the potential response to selection in the non-food supplemented environment (see Fig 6.4A, age 30 days). This is particularly interesting because we know from previous work that selection is generally stronger in the non-food supplemented environment and warmer conditions (Sauve et al. 2023), suggesting we might expect evolution in this context. However, selection also tends to become weaker with ontogeny when we observed differences in heritability or evolvability (Sauve et al. 2023).

At hatching, we found that a high proportion of the phenotypic variance was explained by maternal effects for hatching mass, but not hatching wing length (Figs. 6.2, 6.3). Evolution of nestling traits can also depend on the heritability of parental effects (Kirkpatrick and Lande 1989). Variation among maternal contributions to nestling mass was the highest immediately after hatching, which is when viability selection on nestlings is the strongest. Generally, a low proportion of phenotypic variation was explained by parental effects, and we did not detect differences in among-parent variation across our treatments (Fig. 6.2, 6.3). This is potentially an important finding because maternal effects themselves can be heritable, and have the potential to contribute to a trait's evolutionary response (Mcadam et al. 2002; McAdam and Boutin 2004). Maternal effects have the potential to cascade and increase the response to selection (Pick et al. 2019), but they are also dependent on trade-offs, and the genetic covariance of indirect genetic effects of parents and direct genetic effects (Willham 1972; Cheverud 1984). Estimates of such indirect-direct genetic covariance in wild populations indicate some positive and negative covariances, but covariance alone is generally not enough to prevent an evolutionary response in offspring traits (Mcadam et al. 2002; Wilson et al. 2005; Thomson et al. 2017). A genetic

covariance combined with a trade-off with parental fitness seems to be required to cause evolutionary stasis. Increases in offspring size through maternal effects probably come at some fitness cost to parents. For example, in Eurasian blue tits *Cyanistes caeruleus*, larger nestlings are more likely to survive, but parents that produce larger nestlings are less fecund, suggesting a cost to increased investment in nestlings (Thomson et al. 2017). Future studies should aim to investigate selection on parental effects for body mass as well as the genetic correlation between parental and direct genetic effects for body mass to determine the potential for maternal effects to enhance the evolution of early-life mass traits in kittiwakes.

### **6.5.3 Annual variation and cohort effects**

The higher annual variation of mass and wing length observed in non-food supplemented nestlings indicates a greater impact of year-to-year environmental conditions on non-food supplemented nestlings than on food supplemented nestlings. It is generally agreed that early-life conditions can shape an adult's life-history strategy (Cooper and Kruuk, 2018; Lindström and Lindström, 1999; Spagopoulou et al., 2020), although the direction of these effects is still debated - whether favorable early-life conditions always lead to improved adult vital rates or whether early-life environments that match adult environments result in better adult vital rates (Grafen 1990; Promislow and Harvey 1990; Spagopoulou et al. 2020). Regardless, the increased impact of annual variation on non-food supplemented nestlings has the potential to increase the variability of adult vital rates through cohort effects, if early-life phenotypes translate to differences among adults. Cohort effects, or differences in vital rates among population cohorts, can have a wide range of impacts on population dynamics (Kendall et al., 2011; Cressler et al., 2017), but in many cases are expected to cause instability in population dynamics (Lindström and Kokko, 2002). To identify the impacts of early-life variation in kittiwakes, it will be

important to determine whether differences in mass or wing length caused by annual variation (or other environmental vagaries) are associated with differences in vital rates among cohorts or individuals.

In conclusion, our study found evidence of increased evolvabilities and annual variances in nestling black-legged kittiwakes under non-food supplemented conditions compared to food supplemented conditions. These findings suggest that evolutionary responses may be more rapid in environments with variable resources, although this ultimately depends on how selection operates. Additionally, the increased annual variation we observed raises the question of whether such variation among non-food supplemented nestlings results in increased variation among reproductive adults, and whether cohort effects may impact kittiwake demographics. Our study, along with others like it, highlights the potential impact of food supplementation on evolutionary dynamics, and the need for further investigation into how it affects the rate of evolution in response to ongoing environmental changes in the wild.

**Table 6.1: Age standardized (centered on mean for each age group and divided by the standard deviation) masses for nestling rank (first-hatched vs. second-hatched) and food treatment (food supplemented vs. non-food supplemented).**

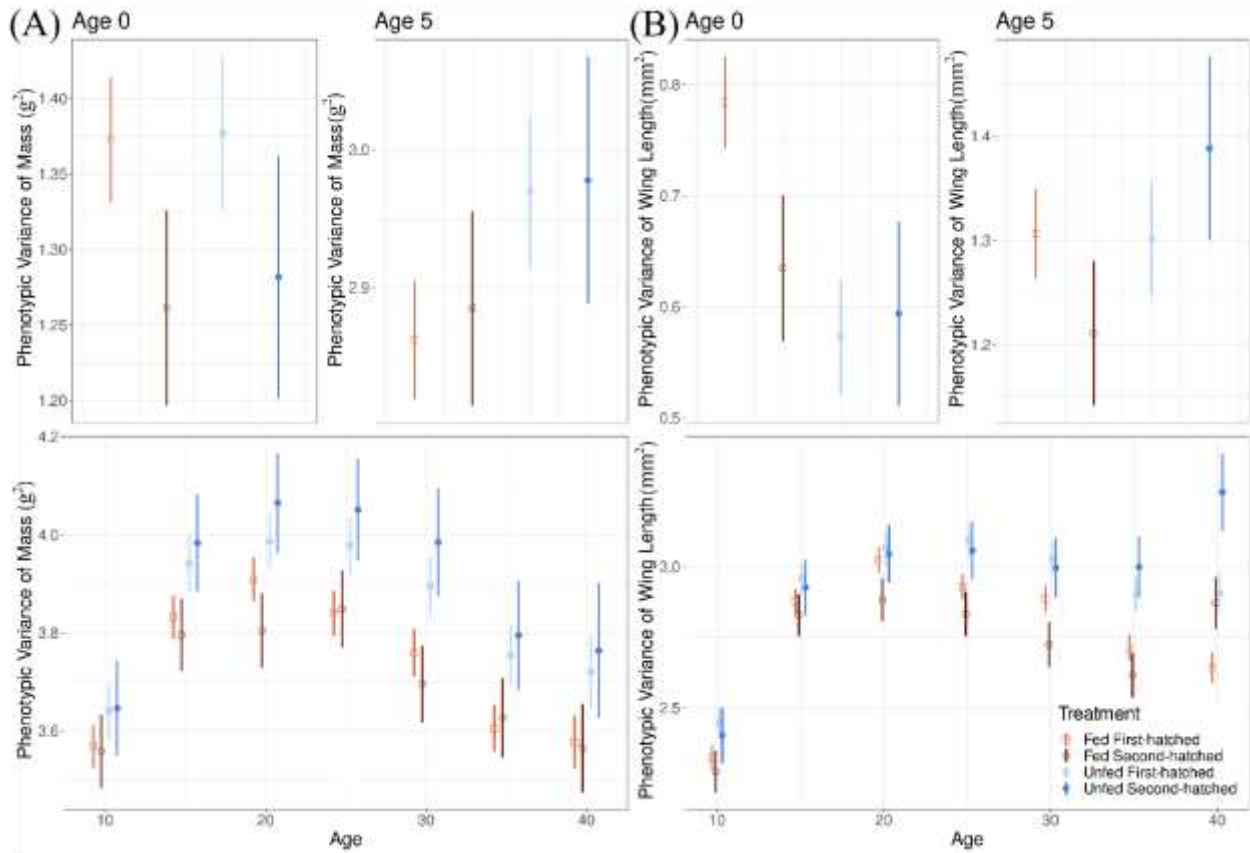
Estimates are reported as the difference from food supplemented first-hatched nestlings (second column). Standard errors (SE) and sample sizes of birds measured for both mass and wing length (see Table 6.2 for wing length estimates) are reports in brackets and after a semi-colon, respectively.

<b>Age Standardized Mass (SE); Sample Size (n)</b>				
<b>Age</b>	<b>Food supplemented</b>		<b>Non-food supplemented</b>	
	<b>Intercept/First-hatched</b>	<b>Second-hatched</b>	<b>First-hatched</b>	<b>Second-hatched</b>
<b>0</b>	0.09 (0.06); n = 1923	-0.34 (0.04); n=1200	-0.04 (0.06); n=1098	-0.16 (0.04); n=738
<b>5</b>	0.06 (0.07); n = 1728	-0.32 (0.04); n=786	-0.07 (0.08); n=1004	-0.47 (0.09); n=575
<b>10</b>	0.06 (0.08); n = 1539	-0.32 (0.04); n=573	-0.17 (0.09); n=954	-0.54 (0.10); n=511
<b>15</b>	0.10 (0.07); n = 1511	-0.29 (0.04); n=531	-0.28 (0.10); n=964	-0.73 (0.10); n=505
<b>20</b>	0.11 (0.07); n = 1416	-0.21 (0.04); n=480	-0.37 (0.10); n=950	-0.84 (0.10); n=490
<b>25</b>	0.18 (0.06); n = 1461	-0.14 (0.05); n=463	-0.46 (0.09); n=910	-0.87 (0.10); n=463
<b>30</b>	0.18 (0.05); n = 1270	-0.04 (0.05); n=422	-0.46 (0.08); n=878	-0.81 (0.09); n=458
<b>35</b>	0.20 (0.05); n = 1176	-0.10 (0.05); n=391	-0.49 (0.09); n=849	-0.72 (0.10); n=439
<b>40</b>	0.12 (0.06); n = 671	-0.06 (0.06); n=439	-0.23 (0.07); n=668	-0.50 (0.09); n=224

**Table 6.2: Age standardized (centered on mean for each age group and divided by the standard deviation) wing length for nestling rank (first-hatched vs. second-hatched) and food treatment (food supplemented vs. non-food supplemented).**

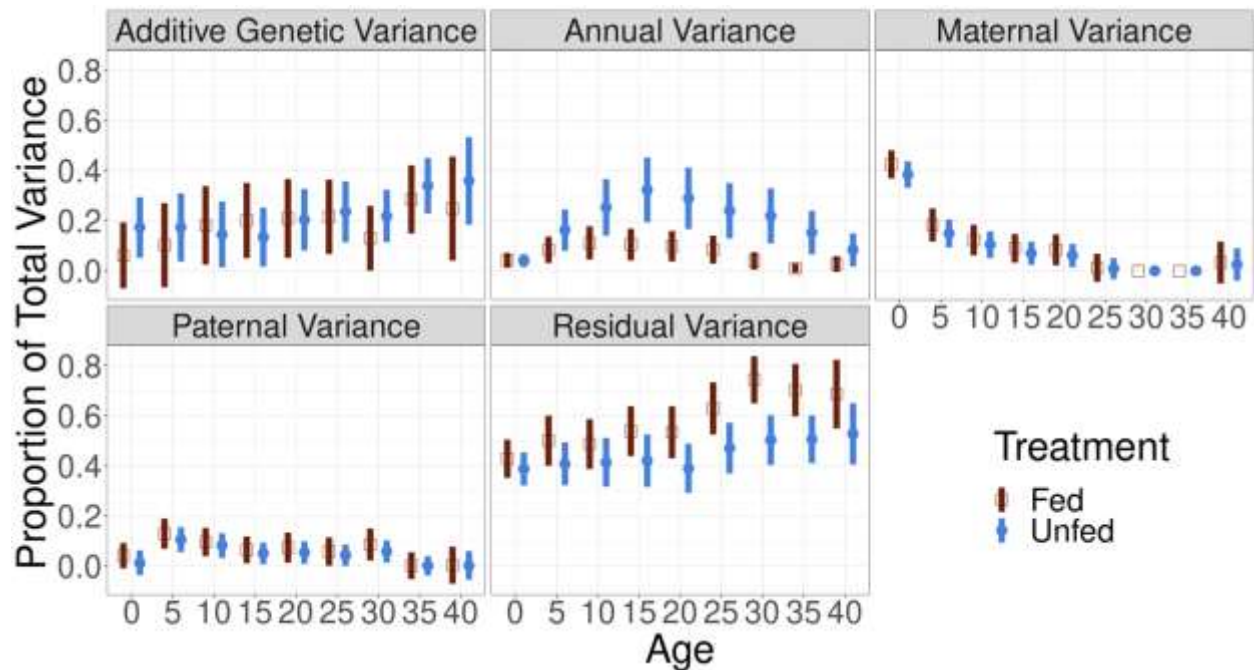
Estimates are reported as the difference from food supplemented first-hatched nestlings (second column). Standard errors (SE) are reported in brackets. Refer to Table 6.1 for sample sizes of each group.

<b>Wing length (SE)</b>				
<b>Age</b>	<b>Food supplemented</b>		<b>Non-food supplemented</b>	
	<b>Intercept/First-hatched</b>	<b>Second-hatched</b>	<b>First-hatched</b>	<b>Second-hatched</b>
0	0.09 (0.11)	-0.25 (0.04)	-0.09 (0.07)	-0.20 (0.07)
5	0.03 (0.08)	-0.26 (0.04)	-0.04 (0.08)	-0.30 (0.08)
10	0.02 (0.08)	-0.27 (0.04)	-0.17 (0.10)	-0.45 (0.11)
15	0.02 (0.08)	-0.27 (0.04)	-0.17 (0.10)	-0.45 (0.11)
20	-0.01 (0.08)	-0.20 (0.04)	-0.15 (0.11)	-0.49 (0.11)
25	1.9E-03 (0.08)	-0.21 (0.04)	-0.19 (0.10)	-0.50 (0.11)
30	0.19 (0.05)	-0.04 (0.05)	-0.47 (0.08)	-0.81 (0.09)
35	0.07 (0.07)	-0.19 (0.04)	-0.27 (0.10)	-0.59 (0.11)
40	0.14 (0.07)	-0.13 (0.04)	-0.38 (0.09)	-0.71 (0.10)



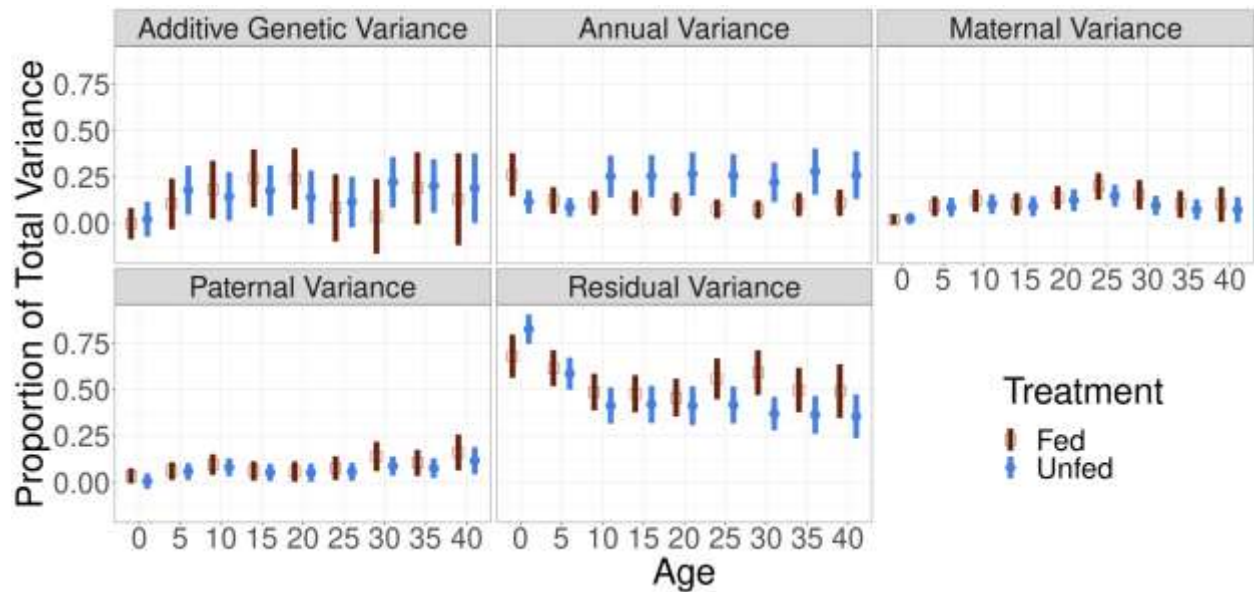
**Figure 6.1: Phenotypic variance of mass (A) and wing length (B) by food treatment and nestling hatching order in black-legged kittiwakes.**

Displayed are the phenotypic variance and 95% confidence intervals for each age-specific measurement. Age 0 and age 5 phenotypic variances are displayed in separate panels to visualize differences among treatment and nestling hatching order groups. Open brown shapes indicate food supplemented nestlings, while closed blue shapes indicate non-food supplemented nestlings. Squares indicate estimates for the first-hatched nestlings and circles indicate estimates for the second-hatched nestlings.



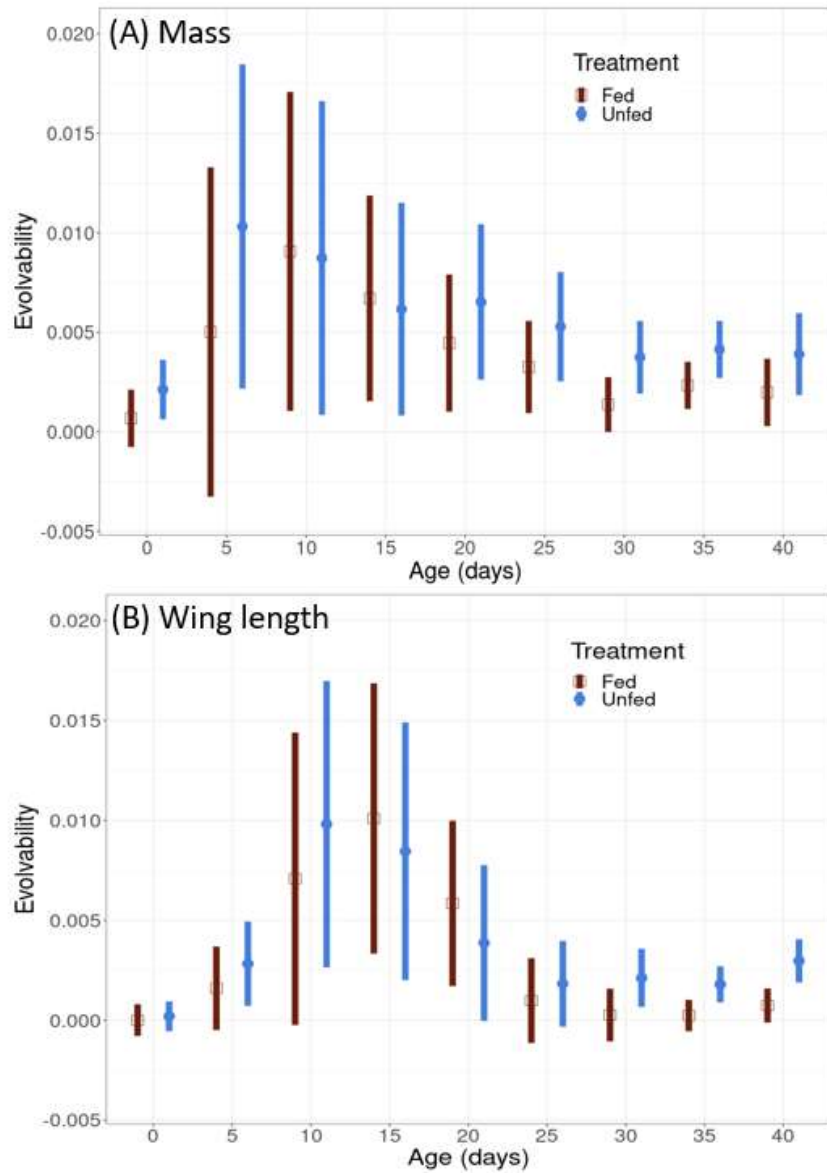
**Figure 6.2: Components of phenotypic variance of mass standardized by total phenotypic variance of mass.**

Each panel title indicates the specific variance component. Each component is standardized by the total phenotypic variance observed for the specific treatment and rank group. Point estimates and 95% percent confidence intervals are displayed for each variance component. Open brown shapes indicate food supplemented nestlings, while closed blue shapes indicate non-food supplemented nestlings. Squares indicate estimates for the first-hatched nestlings and circles indicate estimates for the second-hatched nestlings.



**Figure 6.3: Components of phenotypic variance of wing-length standardized by total phenotypic variance of wing-length.**

Each panel title indicates the specific variance component. Each component is standardized by the total phenotypic variance observed for the specific treatment and rank group. Point estimates and 95% percent confidence intervals are displayed for each variance component. Open brown shapes indicate food supplemented nestlings, while closed blue shapes indicate non-food supplemented nestlings. Squares indicate estimates for the first-hatched nestlings and circles indicate estimates for the second-hatched nestlings.



**Figure 6.4: Evolvabilities of nestling kittiwake mass (A) and wing-length (B).**

Evolvabilities are the traits standardized by age, food treatment, and rank specific averages of squared mass, and indicate the percent change in a trait expected given a standard unit of selection. Point estimates and 95% percent confidence intervals are displayed for each variance component. Open brown shapes indicate food supplemented nestlings, while closed blue shapes indicate non-food supplemented nestlings. Squares indicate estimates for the first-hatched nestlings and circles indicate estimates for the second-hatched nestlings.

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## **Chapter 7 Summary and Conclusions**

The study of phenotypic change has long been a crucial area of interest for evolutionary biologists, plant and animal breeders, and ecologists alike (Parmesan 2006; Charmantier and Gienapp 2014; Walsh and Lynch 2018). By examining evolutionary and ecological dynamics in natural environments, we gain insights into how evolution interacts with ecological processes (Trask et al. 2017; Pemberton et al. 2022). However, predicting trait changes in wild populations remains a challenge (Pujol et al. 2018) due to a lack of understanding and measurement of how genotypes and evolutionary forces interact with the environment (West-Eberhard 2003; Sultan 2015). Despite these difficulties, predicting the responses of wild organisms to environmental change is essential to many fields of biology, with far-reaching implications for academic and practical purposes. Additionally, there is an increasing expectation for scientific research to contribute to predicting, understanding, and mitigating the impacts of human-induced changes on biodiversity (Bradshaw and Bekoff 2001).

In my thesis, I examined three Arctic seabird populations that have experienced varying climatic conditions to contribute to our understanding of how environmental conditions shape offspring traits. Specifically, I provide information that could be used to predict phenotypic change, selection, and evolution of growth traits. However, further research is necessary to determine the significance of my observed changes throughout the life cycle and to assess how trade-offs between parents and offspring may affect our predicted changes in phenotypes and selection.

### **7.1 Changes in avian growth in response to weather conditions are varied**

In chapter 2, I reviewed the literature on the impacts of weather variation on avian growth traits. This chapter offers a summary of the accumulated knowledge on the impacts of climate change

on avian growth and development. Our findings indicated mixed effects of increasing temperatures and rainfall on nestling growth, while increasing wind speeds tend to have negative impacts on open cup nesting species. We also discussed the evolution of nestling growth traits and suggested the need for more estimates of inheritance and selection. While this chapter provides a comprehensive summary of our current understanding of the effects of weather conditions on avian growth, it also highlighted the gaps in our knowledge that require further investigation. Specifically, several unanswered questions relate to the cues and constraints that influence avian growth, the expected changes in selection, and the evolvability of growth traits. In this thesis, I attempt to address some of these gaps by investigating the growth of three high-latitude seabirds. Beyond the thesis, several key questions remain to be investigated, such as the impact of variation in avian growth on adult fitness, how parents might alter investment in offspring because of changing environments, and how selection operates on parental investment in a changing climate (e.g. Thomson et al. 2017).

## **7.2 Specific windows predict components of seabird growth, but they seem unlikely to remain constant over time**

One unanswered question identified in chapter 2 was *when* during the breeding season nestling growth is most affected by environmental conditions. To tackle this challenge, in chapter 3 we use three long-term seabird datasets combined with a sliding window approach to determine when and how environmental variation (e.g. sea-surface temperature, ice-cover) impacts components of nestling growth (Hadfield 2010; van de Pol et al. 2016; Bürkner 2017; Gomulkiewicz et al. 2018). We chose these three species because environmental and biological changes occurred over the study of all three seabird species. Our approach allowed us to predict the impacts of changing climate on chick growth in these species. It also provided information

about how offspring growth might change with climate, and identified windows of climatic variation that could be used in future studies of natural selection acting on growth (Chapter 5). Furthermore, this work could be informative for conservation managers in identifying periods that most strongly impact the ability of seabirds to raise offspring.

In chapter 3, we used a sliding window approach to infer about growth under warming conditions. We used the sliding window approach method to identify when sea-surface and air temperatures correlate with growth of black-legged kittiwakes *Rissa tridactyla* in the Northeast Pacific. Analysis of the growth data showed that warmer conditions can have both positive and negative effects on nestling growth, depending on hatching order, and that food supplementation and nestling competition influenced the strength of these effects. Our study identified specific windows when environmental variation directly or indirectly affects growth and highlights that nestlings in shared nests are most affected by warming conditions.

In chapter 4, we evaluated whether windows identified for kittiwakes, thick billed murre *Uria lomvia*, and glaucous-winged gulls *Larus glaucescens* changed between years. Using multiple multi-decadal datasets, we determined the periods of within-year environmental variation that predicted growth in the three seabird species. We evaluated whether these periods changed over time to predict future growth under climate change. Our findings showed that the timing and type of environmental predictors of growth can change over time, with evidence of changes in all populations studied. Environmental models predicted that warming conditions will decrease growth rates and body sizes, with potential consequences for fledging rates.

Our study highlighted the need to investigate whether environmental determinants of trait variation commonly shift in a changing climate and determine whether these shifts have implications for adaptation to novel environments. Contemporary windows might provide

predictions for nestling growth, but a great deal of work is still needed to understand and interpret these windows. We still do not know if these windows are the best predictors of growth because we have identified a critical window for seabird prey or if we have identified time periods where nestlings are most sensitive to food variation. Further, are the windows just general predictors of favourable or unfavourable breeding seasons or are they directly linked to food resources? Data from annual collections of prey items and data from fishing vessels in nearby ocean regions might hint at an answer. Further, it would be interesting to evaluate how low food resources differentially affect nestling morphology or growth at different stages of development. Regardless, our predictions provide a first attempt at determining how growth might change under future warming conditions, but refinement of these predictions will be valuable.

### **7.3 The strongest selection for nestling mass tends to occur early in ontogeny when nestlings are competing with siblings and when food resources are low**

Because natural selection is the driving force of adaptive change, my fifth chapter provides information needed to make evolutionary predictions regarding adaptive change in chick traits. Measuring selection is required to understand to predict the evolutionary response of a trait. Because the environment during early life can impact the phenotypic expression of a trait in later life, changes in the phenotype have the potential to impact population dynamics (Moore and Martin 2019).

In this chapter, we identified a relationship between natural selection and environmental conditions (the relevant window of environment was identified in Chapters 3 and 4) for nestling black-legged kittiwakes. We examined 25 years of data on black-legged kittiwakes, finding that larger and heavier nestlings are more likely to survive, younger nestlings experienced stronger

selection, and warming conditions increased selection on nestling mass. Resource dynamics likely cause variability in selection, and local environmental heterogeneity could buffer selection from broader climatic changes.

Our work highlights that understanding the interaction between local conditions and broader climate change could improve our ability to predict future selection gradients. This is a potentially important finding as a common human interaction with wildlife is food supplementation. It raises the question of how our food supplementation might alter the response to climate change. Further, it will be interesting to determine whether strong selection is commonly experienced by younger siblings or nestlings in low food environments.

We, and researchers in general, are often missing a large piece of the puzzle in that we do not measure how selection acts on parental investment (Thomson and Hadfield 2017; Thomson et al. 2017). Depending on how environmental conditions affect parental fitness, faster or slower life-histories may be favored. For example, we noted that first-hatched nestlings are less perturbed by environmental conditions and faced weaker selection than second-hatched nestlings. Selection may favor parents that produce smaller broods and have increased lifespans, or if climate impacts parent mortality, selection may favour parents that invest a great deal in a single reproductive event. Understanding selection on parental life-history strategies will be a large component of understanding how future climate impacts growth phenotypes and selection on growth phenotypes. Further, investigating whether selection on traits remains consistent for post-fledging birds will be important, as measuring selection across life stages is necessary to get a measurement of the total selection acting on any trait (e.g. Price and Grant 1984).

#### **7.4 Food supplementation reduces annual phenotypic variance and potentially additive genetic variance**

My last chapter investigated associations between environmental conditions and components of phenotypic variation in populations. Current empirical studies provide mixed results, and more research is needed to determine how this variation changes across different traits, taxa, and environments (Charmantier and Garant 2005; Rowiński and Rogell 2017). We found evidence of increased phenotypic and annual variability in the morphology of non-food supplemented nestlings compared to food supplemented nestlings. The higher annual variation observed in non-food supplemented nestlings could have important implications for the demography of adult kittiwakes (Kendall et al. 2011). To identify the impacts of early-life variation in growth in kittiwakes, it will be important to determine whether differences in mass or wing length caused by annual variation are associated with differences in fecundity, longevity, or survival among cohorts or individuals. Many studies are beginning to identify these “carry-over” effects from early-life to reproductive age (e.g. Cooper and Kruuk 2018), so it will be interesting to determine if nestling growth and size impact adults life-history strategy, and whether the non-food supplemented environment produces a more diverse array of adult life-history strategies.

Based on previous findings in wild populations, we predicted lower genetic variation in non-food supplemented kittiwake nestlings, but we found the opposite result with the highest heritabilities for mass and wing length in unfavourable conditions. Comparison with similar studies in arthropods, amphibians, birds, fishes, mammals, and mollusks (Uller et al. 2002; Ernande et al. 2004; Uhl et al. 2004; Charmantier and Garant 2005; Garant et al. 2005) suggests that the observed decrease in genetic variation under resource supplementation is not a general rule. A general rule for how genetic variance is expected to change across conditions may not exist, making predicting phenotypic responses to changing environments difficult under our

current framework. One limitation of our approach is that our “unfavourable” conditions encompass both favourable and unfavourable years. It would be important to compare phenotypic variance components of nestlings from the non-food supplemented conditions that experienced favourable climatic conditions and unfavourable climatic conditions each to phenotypic variance components of our food supplemented nestlings. Relatedly and more generally, our current framework and definitions for environmental conditions might not be specific enough or might not be capturing the axes of environmental variation that are likely to alter additive genetic variance. However, if additive genetic variance is relatively unchanged by resource changes (as indicated in our study) prediction of trait response might be easier because shifting conditions, like climate change, might not continually alter the additive genetic variance of traits.

### **7.5 Understanding and predicting the impacts of changing phenotypes: concluding remarks**

The integration of information on environment relationships with phenotypes, selection, and genetic variation using demographic modelling and climatic niche models is an exciting next step in understanding how both plasticity and evolution allow population persistence (Knight et al. 2008; Forester et al. 2023). Further, these relationships could be studied to understand how environmentally caused changes in phenotypes, selection, and genetic variation within species might affect species-interactions (Bolnick et al. 2011; Cressler et al. 2017). I believe that a promising approach for long-term studies is to develop a system for continual forecasting of traits, interactions, and demography, like weather forecasting (Knight et al. 2008; Vedder et al. 2013; Gauzere et al. 2020). By doing so, we can identify and correct our mistakes to further improve our predictions. While the literature, including my thesis, provides valuable information

on observed changes, it can sometimes fall short of using this information to make quantitative predictions about trait and demographic changes under changing conditions. We should strive towards not only gathering information and describing observed changes, but also using this information to make specific and quantitative predictions about trait and demographic changes. Further, making mistakes in this endeavor should reveal interesting biology as we attempt to determine why phenotypes or species do not respond in the way we might predict.

Advancements in technology have the potential to enhance our ability to predict trait responses in variable and uncontrolled wild settings across a broad range of taxa and environments. With the advent of new technologies in genomics, phenotyping, and computing power, we can now collect larger amounts of phenotypic, genetic, and relatedness data for challenging-to-study species or traits. These advancements could reveal new insights into the complexities of evolution and ecology in natural settings, enabling us to make more accurate predictions about the impacts of environmental changes on biodiversity (Houle et al. 2010; Brisson-Curadeau et al. 2017; Gienapp et al. 2017; Gervais et al. 2019; Madden et al. 2022). These advances are going to be incredibly useful as we seek to conduct long-term studies on a broader range of taxa and types of traits. Hopefully, additional studies like the present work in other taxa (e.g., in under-explored tropical areas and the global south) will improve our ability to generalize about effects of changing environments on phenotypes, selection, and genetic variance.

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## Appendix A: Supplementary Material for Chapter 3

### Models of changes in growth parameters over time

We used four non-linear models to evaluate whether the growth parameter estimates changed over time in our study. For each sibling-food treatment, we ran a model with no random effects and a continuous effect of year for each growth parameter (Supplemental Model 1):

$$W = A \left( 1 + (d - 1) \cdot \exp \left( \frac{-k(t - T)}{\frac{d^d}{1 - d}} \right) \right)^{\frac{1}{1-d}} + \varepsilon, \quad (1)$$

$$A \sim Xb_A,$$

$$k \sim Xb_k,$$

$$T \sim Xb_T,$$

$$d \sim 1$$

where  $X$  is a matrix of the predictor variables for each parameter, and  $b_A$ ,  $b_k$ , and  $b_T$  are vectors of continuous linear and quadratic fixed effects of year.

### Extraction of growth estimates and sliding window evaluation

Our biological traits of interest were the individual deviations from the mean population-level estimates of our growth curve parameters. We estimated the individual deviation from the population mean for the growth parameters ( $A$ ,  $k$ ,  $T$ ) by summing the random effect estimate for a given individual nestling ( $I$ ) and its hatch-year ( $Y$ ; e.g. Aldredge, 2016). We used each individual's extracted random effect estimate as a response variable in our relative sliding window analysis. Few studies have tried to find environmental predictors of individual-level growth parameters, and a challenge exists in carrying forward error in the estimates. We acknowledge that we do not carry forward error in our analysis but running our analysis on the

entire posterior distribution of an estimate would be computationally time-consuming. We evaluated weather variables for air temperature and sea-surface temperature in a time period 120 days before measurement of nestlings when they would be 40 days old (roughly fledging date). We chose this time window because it encompasses weather variation during follicle development, incubation, and nestling growth (Roudybush et al., 1979).

We based our model choice on three indicators of model explanatory power from the ‘climwin’ sliding window analysis (van de Pol et al., 2016): the difference between the Akaike Information Criterion of a given model and that of a model with an intercept only ( $\Delta AIC$ ); the probability of detecting the best windows as a signal just by chance ( $P_C$ ); and the extent to which several windows have similar explanatory power as the top model ( $\%CI$ ). To calculate  $P_C$ , we run five simulation models using different randomizations of the mean phenotype across years. The  $\%CI$  is calculated as the percentage of all tested window models required to reach 95% of the sum of all Akaike weights. In our model selection process, we first chose models that have the smallest  $\Delta AIC$ . We considered models with a  $\Delta AIC$  of  $<2$  to provide equal statistical support (Burnham & Anderson, 1998). Of the top models with the lowest  $\Delta AIC$ , we then choose the models with the lowest confidence set ( $\%CI$ ) and the smallest probability of being observed by chance ( $P_C$ ). If the lowest confidence set and smallest probability disagree, we chose the model with the lowest confidence set. We used the lowest confidence set because our models often had similarly low probabilities of being observed by chance ( $P_C$ ) but differed in the extent to which several models had similar explanatory power ( $\%CI$ ).

### **Interpretation of model interactions**

We restricted our interpretation of interactions to combinations of environmental conditions that occurred in any given year during the 21 years of observations. Suppose our model suggested that nestlings' asymptote is dependent on an interaction of sea-surface and air temperature during

growth. In this case, we only plotted the effects of this interaction across combinations of sea-surface and air temperatures that occurred in a given year of the study— not the most extreme sea-surface and air temperatures we observed in the dataset. For example, in some years of the study, 12°C air temperatures might occur during nestling growth, and in some years, parents might experience 6°C sea-surface temperature during incubation, but in no years did both 12°C air temperatures and 6°C sea-surface temperatures occur during growth.

**Appendix A Table A1:** Growth model estimates and 95% credible intervals for alpha and beta nestlings, and food supplemented (fed) and control (unfed) nests. Results are reported for the asymptote (A), maximum growth rate (k), timing of maximum growth (T), the shape parameter (d), and residual variance ( $\sigma$ ). Raw growth curves are displayed in Figure 3.2, and annual curves predicted from models are in Appendix A Figure A2. Estimates of standard deviations (SD) are presented in square parentheses for variance components.

<b>Treatment</b>	<b>Rank</b>	<b>Population-Level Parameters</b>				
<b>Unfed</b>		<b>A</b>	<b>k</b>	<b>T</b>	<b>d</b>	<b><math>\sigma</math> (SD)</b>
$N_{\text{YEARS}} = 21$	<b>Alpha</b>	405	4.49E-02	13.5	2.07	20.6
$N_{\text{IND}} = 1190$		[397, 413]	[4.28E-02, 4.72E-02]	[12.8, 14.1]	[1.99, 2.14]	[20.2, 21.0]
$N_{\text{YEARS}} = 21$	<b>Beta</b>	379	4.33E-02	13.2	1.90	19.8
$N_{\text{IND}} = 788$		[359, 399]	[4.09E-02, 4.58E-02]	[12.5, 14.0]	[1.80, 2.00]	[19.3, 20.4]
<b>Fed</b>						
$N_{\text{YEARS}} = 20$	<b>Alpha</b>	421	4.87E-02	13.3	2.26	18.0
$N_{\text{IND}} = 994$		[416, 425]	[4.74E-02, 5.00E-02]	[12.9, 13.7]	[2.19, 2.33]	[17.7, 18.4]
$N_{\text{YEARS}} = 20$	<b>Beta</b>	418	4.85E-02	14.0	2.38	17.0
$N_{\text{IND}} = 676$		[413, 422]	[4.73E-02, 4.99E-02]	[13.6, 14.4]	[2.29, 2.47]	[16.5, 17.4]
<b>Treatment or Rank</b>	<b>Annual Variation (SD)</b>			<b>Among Individual Variation (SD)</b>		
<b>Unfed</b>	<b>A</b>	<b>k</b>	<b>T</b>	<b>A</b>	<b>k</b>	<b>T</b>
<b>Alpha</b>	16.5 [10.9, 24.2]	5.03E-03 [3.67E-03, 6.97E-03]	1.33 [0.952, 1.86]	36.2 [33.7, 38.4]	5.03E-03 [3.67E-03, 6.97E-02]	1.95 [1.83, 2.10]
<b>Beta</b>	37.3 [23.9, 57.2]	4.84E-03 [3.22E-03, 7.03E-03]	1.48 [0.929, 2.25]	44.4 [40.2, 49.0]	5.37E-03 [3.72E-03, 6.12E-02]	1.97 [1.76, 2.19]
<b>Alpha</b>	8.15 [4.29, 13.2]	2.68E-03 [1.80E-03, 3.95E-03]	0.737 [0.476, 1.10]	32.6 [30.7, 34.7]	4.40E-03 [4.00E-03, 4.83E-02]	2.19 [2.05, 2.33]
<b>Beta</b>	4.50 [2.36E-03, 10.9]	2.40E-03 [1.50E-03, 3.64E-03]	0.746 [0.462, 1.14]	35.2 [32.6, 38.2]	3.90E-03 [3.35E-03, 4.48E-02]	2.10 [1.93, 2.28]
<b>Treatment or Rank</b>	<b>Annual Correlations</b>			<b>Among Individual Correlations</b>		
<b>Unfed</b>	<b>A, k</b>	<b>A, T</b>	<b>k, T</b>	<b>A, k</b>	<b>A, T</b>	<b>k, T</b>
<b>Alpha</b>	0.61 [0.22, 0.86]	-0.48 [-0.81, 0.03]	-0.92 [-0.98, -0.80]	0.10 [-0.03, 0.24]	0.09 [0.002, 0.18]	-0.96 [-0.99, -0.93]
<b>Beta</b>	0.31 [-0.18, 0.72]	-0.071 [-0.57, 0.44]	-0.87 [-0.97, -0.65]	-0.15 [-0.33, 0.04]	0.42 [0.30, 0.53]	-0.94 [-0.98, -0.89]
<b>Alpha</b>	0.37 [-0.16, 0.78]	-0.004 [-0.54, 0.52]	-0.74 [-0.92, -0.40]	0.13 [2.0E-04, 0.25]	0.068 [-0.02, 0.15]	-0.96 [-0.99, -0.93]
<b>Beta</b>	0.14 [-0.72, 0.84]	0.06 [-0.77, 0.79]	-0.87 [-0.99, 0.61]	0.103 [-0.08, 0.28]	0.17 [0.05, 0.28]	-0.94 [-0.98, 0.88]

**Appendix A Table A2:** Results from a non-linear model of **unfed alpha kittiwakes** with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. A prefix for each predictor is included to indicate which parameter the term corresponds to. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	1.946	0.065	1.824	2.072	1	952	1065
A_Intercept	4.188	0.017	4.155	4.221	1	1051	989
<b>A_Year</b>	<b>-0.007</b>	0.002	<b>-0.01</b>	<b>-0.003</b>	1	1306	1534
<b>A_IYearE2</b>	<b>-0.002</b>	0	<b>-0.002</b>	<b>-0.001</b>	1	1343	1463
k_Intercept	4.537	0.057	4.42	4.649	1	1069	1158
<b>k_Year</b>	<b>-0.065</b>	0.007	<b>-0.078</b>	<b>-0.051</b>	1	1493	1390
k_IYearE2	0.001	0.001	-0.002	0.003	1	1275	1652
T_Intercept	12.387	0.177	12.031	12.724	1	1036	1171
<b>T_Year</b>	<b>0.119</b>	0.01	<b>0.099</b>	<b>0.138</b>	1	1220	1219
<b>T_IYearE2</b>	<b>0.004</b>	0.002	<b>0</b>	<b>0.007</b>	1	1682	1585

**Appendix A Table A3:** Results from a linear model of **unfed beta kittiwakes** with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	1.764	0.077	1.618	1.913	1.005	978	1269
A_Intercept	4.213	0.029	4.159	4.271	1.003	1048	1194
<b>A_Year</b>	<b>0.017</b>	<b>0.003</b>	<b>0.01</b>	<b>0.024</b>	1.002	1061	1157
<b>A_IYearE2</b>	<b>-0.004</b>	<b>0.001</b>	<b>-0.006</b>	<b>-0.003</b>	1.001	1104	1327
k_Intercept	4.633	0.084	4.467	4.798	1.004	1066	1246
<b>k_Year</b>	<b>-0.071</b>	<b>0.01</b>	<b>-0.091</b>	<b>-0.051</b>	1	1144	1014
k_IYearE2	-0.004	0.002	-0.007	0	1.002	1367	1430
T_Intercept	11.753	0.239	11.289	12.219	1.002	1056	1045
<b>T_Year</b>	<b>0.176</b>	<b>0.018</b>	<b>0.141</b>	<b>0.213</b>	1	1090	1122
<b>T_IYearE2</b>	<b>0.013</b>	<b>0.004</b>	<b>0.005</b>	<b>0.022</b>	1.001	1229	1442

**Appendix A Table A4:** Results from a linear model of **fed alpha kittiwakes** with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.157	0.067	2.025	2.287	1	851	1024
A_Intercept	4.209	0.015	4.179	4.24	1	1144	1211
A_Year	-0.001	0.001	-0.004	0.002	1	1484	1370
A_IYearE2	0.00007	0.00027	-0.0005	0.001	1	1543	1660
k_Intercept	4.705	0.06	4.587	4.822	1	1091	1332
<b>k_Year</b>	<b>-0.028</b>	<b>0.006</b>	<b>-0.04</b>	<b>-0.016</b>	1	1533	1555
k_IYearE2	0.001	0.001	-0.001	0.004	1	1599	1497
T_Intercept	12.97	0.158	12.653	13.273	1	914	1226
<b>T_Year</b>	<b>0.049</b>	<b>0.009</b>	<b>0.032</b>	<b>0.065</b>	1	1442	1322
T_IYearE2	-0.002	0.001	-0.005	0.001	1	1896	1527

**Appendix A Table A5:** Results from a linear model of **fed beta kittiwakes** with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.26239	0.09092	2.0903	2.44317	1	903	834
A_Intercept	4.22442	0.02047	4.18538	4.26457	1	988	936
A_Year2	0.0007	0.00202	-0.00336	0.00479	1	1299	1347
<b>A_IYearE2</b>	<b>-0.00088</b>	<b>0.00039</b>	<b>-0.00165</b>	<b>-0.00011</b>	1	1410	1622
k_Intercept	4.71758	0.0796	4.56321	4.87433	1	981	1318
<b>k_Year2</b>	<b>-0.03412</b>	<b>0.00825</b>	<b>-0.05143</b>	<b>-0.01846</b>	1	1370	1230
k_IYearE2	0.00185	0.00157	-0.0013	0.00495	1	1422	1514
T_Intercept	13.75019	0.21386	13.32091	14.16874	1	1021	1019
<b>T_Year2</b>	<b>0.07473</b>	<b>0.01186</b>	<b>0.05127</b>	<b>0.09792</b>	1	1110	1078
<b>T_IYearE2</b>	<b>-0.00565</b>	<b>0.00232</b>	<b>-0.01011</b>	<b>-0.00108</b>	1	1873	1543

**Appendix A Table A6:** Results from a non-linear mixed model of **unfed alpha nestlings** with a continuous linear effect of the number of days **overlapping with a beta nestling** fit as a predictor for each growth parameter. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept terms where 95% confidence intervals did not overlap zero.

Group-Level ~ChickID	Effects:						
	Number Estimate	of Est.Error	levels: I-95%CI u-95%CI		Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.359	0.012	0.337	0.383	1	3100	5472
sd(T_Intercept)	1.917	0.067	1.789	2.053	1	2330	4631
sd(k_Intercept)	0.440	0.025	0.391	0.489	1	3881	6696
cor(A_Intercept, T_Intercept)	0.090	0.044	0.003	0.176	1	1782	3386
cor(A_Intercept,k_Intercept)	0.104	0.069	-0.030	0.239	1	2747	5058
cor(T_Intercept,k_Intercept)	-0.963	0.017	-0.988	-0.923	1	3773	6189
~Year	Number Estimate	of Est.Error	levels: I-95%CI u-95%CI		Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.164	0.035	0.107	0.243	1	2549	5075
sd(T_Intercept)	1.173	0.215	0.824	1.678	1	3539	4893
sd(k_Intercept)	0.482	0.083	0.348	0.669	1	3932	5404
cor(A_Intercept, T_Intercept)	-0.450	0.208	-0.788	0.006	1	2820	4326
cor(A_Intercept,k_Intercept)	0.592	0.171	0.198	0.852	1	3215	4953
cor(T_Intercept,k_Intercept)	-0.900	0.056	-0.971	-0.759	1	4502	5515
Population-Level	Estimate	Est.Error	I-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.077	0.037	2.005	2.149	1	18314	7160
A_Intercept	4.038	0.041	3.958	4.117	1	2885	5356
A_BetaOverlap	0.001	0.001	-0.001	0.002	1	2560	4582
T_Intercept	13.855	0.282	13.307	14.414	1	3793	5543
<b>T_BetaOverlap</b>	<b>-0.029</b>	<b>0.005</b>	<b>-0.038</b>	<b>-0.020</b>	<b>1</b>	<b>2788</b>	<b>4924</b>
k_Intercept	4.431	0.110	4.219	4.646	1	3781	5515
<b>k_BetaOverlap</b>	<b>0.004</b>	<b>0.002</b>	<b>0.001</b>	<b>0.007</b>	<b>1</b>	<b>4820</b>	<b>7032</b>
Family	Specific	Parameters:					
sigma	20.625	0.189	20.254	21.001	1	8525	8075

**Appendix A Table A7:** Growth model estimates for **fed alpha nestlings** with an effect of the number of days **overlapping with a beta nestling**. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept terms where 95% confidence intervals did not overlap zero.

Group-Level ~ChickID	Effects:				Rhat	Bulk_ESS	Tail_ESS
	(Number Estimate	of Est.Error	levels: l-95%CI	989) u-95%CI			
sd(A_Intercept)	0.324	0.010	0.304	0.345	1	3325	5876
sd(k_Intercept)	0.452	0.028	0.403	0.512	1	520	1761
sd(T_Intercept)	2.144	0.072	2.008	2.288	1	2771	4371
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.086</b>	<b>0.076</b>	<b>-0.072</b>	<b>0.228</b>	<b>1</b>	<b>1303</b>	<b>2359</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.092</b>	<b>0.045</b>	<b>0.003</b>	<b>0.181</b>	<b>1</b>	<b>1558</b>	<b>3033</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.957</b>	<b>0.019</b>	<b>-0.986</b>	<b>-0.915</b>	<b>1</b>	<b>81</b>	<b>1049</b>
~Year	(Number Estimate	of Est.Error	levels: l-95%CI	20) u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.082	0.023	0.043	0.135	1	2051	2577
sd(k_Intercept)	0.261	0.054	0.174	0.383	1	4935	5271
sd(T_Intercept)	0.706	0.156	0.454	1.061	1	3479	5292
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.396</b>	<b>0.251</b>	<b>-0.157</b>	<b>0.812</b>	<b>1</b>	<b>2238</b>	<b>4168</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>-0.079</b>	<b>0.285</b>	<b>-0.613</b>	<b>0.470</b>	<b>1</b>	<b>2453</b>	<b>4110</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.710</b>	<b>0.149</b>	<b>-0.914</b>	<b>-0.344</b>	<b>1</b>	<b>5839</b>	<b>6812</b>
Population-Level	Effects:				Rhat	Bulk_ESS	Tail_ESS
	Estimate	Est.Error	l-95%CI	u-95%CI			
d_Intercept	2.278	0.037	2.205	2.352	1	20436	7063
A_Intercept	4.187	0.027	4.134	4.241	1	3631	5583
A_BetaOverlap	0.001	0.001	0.000	0.003	1	2577	4864
k_Intercept	4.757	0.070	4.617	4.896	1	5939	6906
<b>k_BetaOverlap</b>	<b>0.006</b>	<b>0.001</b>	<b>0.004</b>	<b>0.009</b>	<b>1</b>	<b>4925</b>	<b>7231</b>
T_Intercept	13.944	0.208	13.544	14.364	1	5482	6373
<b>T_BetaOverlap</b>	<b>-0.033</b>	<b>0.004</b>	<b>-0.042</b>	<b>-0.025</b>	<b>1</b>	<b>3237</b>	<b>5274</b>
Family	Specific Estimate	Parameters: Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sigma	18.502	0.185	18.147	18.870	1	2465	6079

**Appendix A Table A8: Results of climwin analysis.** Horizontal sections are divided into nestling seniority (alpha or beta), and food treatment (unfed or fed) while the weather variable analyzed is divided into vertical sections (Sea-surface temperature (SST) on the left and air temperature on the right). For each treatment, seniority category, and weather variable the results from the best model for each summary statistic are displayed (Model). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc) , and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Asymptote, Timing of Maximum Growth/Inflection Point, and the maximum growth rate).

SST						Temperature						
Unfed	Alpha	BestMode		Pc	%Confidence	Unfed	Alpha	Air	BestMode		Pc	%Confidence
Model	$\Delta$ AIC	lOpen	lClose			Model	$\Delta$ AIC	lOpen	lClose			
Asymptote						Asymptote						
Mean	-118.8	120	0	2.0E-03	8	Mean	-126.3	61	47	2.0E-03	6	
Max	-122.0	119	10	1.5E-03	11	<b>Max</b>	<b>-147.2</b>	<b>114</b>	<b>11</b>	<b>2.7E-03</b>	<b>12</b>	
Min	-118.5	120	119	1.6E-03	1	Min	-117.2	53	51	1.1E-03	2	
QuadMean	-119.5	120	0	4.7E-03	11	QuadMean	-124.8	61	47	7.6E-03	10	
QuadMax	-121.8	96	91	4.7E-03	11	QuadMax	-146.5	114	11	3.6E-03	11	
<b>QuadMin</b>	<b>-120.7</b>	<b>14</b>	<b>2</b>	<b>1.9E-03</b>	<b>4</b>	QuadMin	-115.2	53	51	3.3E-03	4	
Inflection Point						Inflection Point						
Mean	-205.4	95	89	1.1E-03	2	Mean	-284.7	120	63	1.4E-03	1	
Max	-237.3	119	91	1.3E-03	1	Max	-259.7	106	91	1.4E-03	1	
Min	-196.9	93	93	1.2E-03	1	Min	-232.7	120	64	1.3E-03	2	
QuadMean	-224.6	95	89	1.8E-03	1	QuadMean	-290.9	120	64	1.5E-03	1	
<b>QuadMax</b>	<b>-264.0</b>	<b>119</b>	<b>90</b>	<b>1.3E-03</b>	<b>1</b>	QuadMax	-262.4	106	91	1.7E-03	1	
QuadMin	-212.8	93	93	1.3E-03	1	<b>QuadMin</b>	<b>-309.6</b>	<b>97</b>	<b>68</b>	<b>5.1E-03</b>	<b>3</b>	
Growth Rate						Growth Rate						
Mean	-281.9	95	90	1.7E-03	1	Mean	-444.0	116	63	1.2E-03	2	
Max	-331.2	107	91	1.0E-03	1	Max	-372.5	40	25	1.1E-03	1	
Min	-273.9	93	93	1.8E-03	0	Min	-389.0	106	65	1.9E-03	8	
QuadMean	-308.5	95	89	1.8E-03	1	QuadMean	-462.2	120	64	1.6E-03	1	
<b>QuadMax</b>	<b>-375.6</b>	<b>119</b>	<b>91</b>	<b>9.9E-04</b>	<b>1</b>	QuadMax	-370.5	40	25	1.6E-03	1	

QuadMin	-294.9	93	93	8.7E-04	0	QuadMin	-556.2	97	68	2.0E-03	3
Unfed	Beta	SST				Unfed	Beta	Air	Temperature		
<b>Asymptote</b>						<b>Asymptote</b>					
Model	ΔAIC	BestMode l Open	BestMode l Close	Pc	%Confide nce	Model	ΔAIC	BestMode l Open	BestMode l Close	Pc	%Confide nce
Mean	-287.1	120	0	2.0E-03	4	Mean	-317.2	63	6	1.0E-03	2
Max	-281.8	60	27	1.5E-03	4	Max	-318.1	101	51	1.5E-03	4
Min	-274.1	31	0	1.0E-03	1	Min	-295.2	55	40	1.1E-03	1
<b>QuadMean</b>	<b>-317.9</b>	<b>120</b>	<b>0</b>	<b>1.9E-03</b>	<b>3</b>	<b>QuadMean</b>	<b>-332.3</b>	<b>62</b>	<b>6</b>	<b>1.7E-03</b>	<b>1</b>
QuadMax	-286.0	60	27	7.3E-03	9	QuadMax	-324.5	100	0	6.9E-03	8
QuadMin	-272.8	31	0	2.2E-03	9	QuadMin	-293.4	55	40	2.7E-03	1
<b>Inflection Point</b>						<b>Inflection Point</b>					
Mean	-139.7	94	94	1.1E-03	1	Mean	-197.7	120	62	1.3E-03	3
<b>Max</b>	<b>-155.6</b>	<b>114</b>	<b>92</b>	<b>1.2E-03</b>	<b>1</b>	Max	-193.0	119	102	1.1E-03	1
Min	-139.7	94	94	1.2E-03	1	Min	-189.3	106	94	2.9E-03	12
QuadMean	-137.9	94	94	1.4E-03	1	QuadMean	-197.2	120	116	2.4E-03	3
QuadMax	-153.6	114	92	1.3E-03	1	QuadMax	-196.0	119	117	1.3E-03	1
QuadMin	-137.9	94	94	3.0E-03	1	<b>QuadMin</b>	<b>-261.2</b>	<b>107</b>	<b>0</b>	<b>3.3E-03</b>	<b>1</b>
Growth Rate						Growth Rate					
Mean	-168.3	94	94	1.3E-03	1	Mean	-272.7	102	93	1.2E-03	1
<b>Max</b>	<b>-183.7</b>	<b>116</b>	<b>93</b>	<b>1.2E-03</b>	<b>1</b>	Max	-215.2	110	88	1.2E-03	2
Min	-168.3	94	94	9.9E-04	1	Min	-321.3	104	93	1.2E-03	1
QuadMean	-166.4	94	94	1.6E-03	1	QuadMean	-271.3	102	93	1.8E-03	1
QuadMax	-182.8	116	93	2.0E-03	1	QuadMax	-213.7	110	88	2.3E-03	2
QuadMin	-166.4	94	94	1.6E-03	1	<b>QuadMin</b>	<b>-390.2</b>	<b>99</b>	<b>70</b>	<b>4.5E-03</b>	<b>5</b>
Fed	Alpha	SST				Fed	Alpha	Air	Temperature		
<b>Asymptote</b>						<b>Asymptote</b>					
Model	ΔAIC	BestMode l Open	BestMode l Close	Pc	%Confide nce	Model	ΔAIC	BestMode l Open	BestMode l Close	Pc	%Confide nce
Mean	-25.9	38	4	2.8E-02	38	Mean	-23.8	11	11	1.7E-02	31

Max	-29.6	117	8	1.1E-02	26	Max	-24.0	36	11	4.1E-02	42
Min	-26.3	22	19	3.3E-03	14	Min	-23.8	11	11	2.3E-03	9
QuadMean	-30.7	38	0	7.5E-03	16	QuadMean					
QuadMax	-30.7	46	3	5.2E-03	19	QuadMax	-25.0	11	11	5.8E-02	43
<b>QuadMin</b>	<b>-30.1</b>	<b>20</b>	<b>6</b>	<b>3.8E-03</b>	<b>8</b>	<b>QuadMin</b>	<b>-31.6</b>	<b>36</b>	<b>2</b>	<b>2.5E-03</b>	<b>6</b>
<b>Inflection Point</b>						<b>Inflection Point</b>					
Mean	-28.9	93	90	2.0E-03	9	Mean	-31.4	119	60	7.1E-03	23
Max	-30.5	108	92	1.6E-03	4	Max	-24.0	108	92	1.7E-03	6
Min	-30.0	94	86	2.1E-03	9	<b>Min</b>	<b>-46.3</b>	<b>117</b>	<b>55</b>	<b>1.7E-03</b>	<b>6</b>
QuadMean	-32.6	94	89	2.9E-03	5	QuadMean	-35.9	120	64	3.4E-03	9
<b>QuadMax</b>	<b>-37.0</b>	<b>108</b>	<b>92</b>	<b>2.7E-03</b>	<b>4</b>	<b>QuadMax</b>	<b>-36.3</b>	<b>73</b>	<b>56</b>	<b>1.6E-03</b>	<b>5</b>
QuadMin	-31.6	94	87	1.9E-03	7	QuadMin	-45.3	117	55	2.9E-03	7
<b>Growth Rate</b>						<b>Growth Rate</b>					
Mean	-95.0	94	89	1.8E-03	7	Mean	-106.0	119	55	2.1E-03	9
Max	-104.1	120	92	1.1E-03	1	Max	-106.7	36	5	1.3E-03	2
Min	0.0	94	85	1.6E-03	4	Min	-107.5	104	94	2.0E-03	7
QuadMean	-103.7	31	28	5.2E-03	14	QuadMean	-105.5	119	64	7.1E-03	20
<b>QuadMax</b>	<b>-116.3</b>	<b>114</b>	<b>22</b>	<b>4.3E-03</b>	<b>13</b>	<b>QuadMax</b>	<b>-124.9</b>	<b>31</b>	<b>5</b>	<b>2.0E-03</b>	<b>2</b>
QuadMin	-100.7	28	28	1.7E-03	4	QuadMin	-123.5	117	70	4.3E-03	12
<b>Fed</b>	<b>Beta</b>	<b>SST</b>				<b>Fed</b>	<b>Beta</b>	<b>Air</b>	<b>Temperature</b>		
<b>Asymptote</b>						<b>Asymptote</b>					
Model						Model					
Mean	-12.7	120	120	6.0E-01	84	Mean	-6.3	51	50	6.2E-01	86
Max	-12.7	120	120	5.5E-01	81	Max	-8.4	20	10	2.1E-01	65
Min	-12.7	120	120	4.1E-01	81	Min	-5.9	50	50	7.3E-01	90
QuadMean	-11.4	120	120	5.3E-01	76	QuadMean	-7.9	13	3	2.4E-01	66
QuadMax	-11.4	120	120	4.8E-01	76	QuadMax	-9.0	20	9	3.5E-01	69
QuadMin	-12.4	13	4	2.2E-01	60	QuadMin	-11.2	7	3	1.1E-01	54

<b>Inflection Point</b>					<b>Inflection Point</b>						
Mean	-31.4	96	92	2.2E-03	9	Mean	-40.0	117	63	3.7E-03	13
Max	-37.1	113	92	1.3E-03	3	Max	-38.4	109	94	1.4E-03	3
Min	-31.4	96	92	1.9E-03	7	Min	-50.2	104	93	7.4E-03	22
QuadMean	-34.9	49	19	5.4E-03	16	QuadMean	-42.1	103	93	1.9E-02	22
<b>QuadMax</b>	<b>-46.3</b>	<b>120</b>	<b>31</b>	<b>2.9E-03</b>	<b>11</b>	QuadMax	-40.7	109	94	8.9E-03	16
QuadMin	-38.8	31	18	9.7E-03	10	<b>QuadMin</b>	<b>-56.4</b>	<b>108</b>	<b>74</b>	<b>4.1E-03</b>	<b>12</b>
<b>Growth Rate</b>					<b>Growth Rate</b>						
Mean	-67.7	116	91	1.4E-03	5	Mean	-77.6	100	93	2.5E-03	10
Max	-79.0	120	93	1.2E-03	2	Max	-92.9	26	2	1.4E-03	4
Min	-67.0	94	93	1.5E-03	4	Min	-101.1	104	95	1.3E-03	1
QuadMean	-84.5	31	19	2.9E-03	8	QuadMean	-94.9	103	93	1.3E-03	1
<b>QuadMax</b>	<b>-93.0</b>	<b>120</b>	<b>93</b>	<b>2.5E-03</b>	<b>9</b>	QuadMax	-108.1	26	3	1.5E-03	2
QuadMin	-85.9	31	19	2.7E-03	1	<b>QuadMin</b>	<b>-110.7</b>	<b>108</b>	<b>74</b>	<b>2.6E-03</b>	<b>6</b>

**Appendix A Table A9: Results of climwin analysis for alpha nestling models with beta overlap.** Horizontal sections are divided into nestling seniority (alpha or beta), and food treatment (unfed or fed) while the weather variable analyzed is divided into vertical sections (Sea-surface temperature (SST) on the left and air temperature on the right). For each treatment, seniority category, and weather variable the results from the best model for each summary statistic are displayed (Model). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance ( $P_c$ ), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Asymptote, Timing of Maximum Growth/Inflection Point, and the maximum growth rate).

Unfed	Alpha	SST				Unfed	Alpha	Air				Temperature
<b>Asymptote</b>						<b>Asymptote</b>						
Model	$\Delta AIC$	BestModel Open	BestModel Close	$P_c$	%Confidence	Model	$\Delta AIC$	BestModel Open	BestModel Close	$P_c$	%Confidence	
<b>Mean</b>	<b>-143.1</b>	<b>98</b>	<b>0</b>	<b>4.0E-03</b>	<b>10</b>	<b>Mean</b>	<b>-146.8</b>	<b>120</b>	<b>0</b>	<b>3.0E-03</b>	6	
Max	-135.5	60	52	4.0E-03	13	Max	-135	120	30	2.0E-03	<b>6</b>	
Min	-128.5	52	52	1.0E-03	2	Min	-127.7	57	56	1.0E-03	1	
QuadMean	-141.1	98	0	4.0E-03	12	QuadMean	-145.1	120	0	2.0E-03	3	
QuadMax	-133.7	60	52	5.0E-03	14	QuadMax	-136.3	120	30	3.0E-03	5	
QuadMin	-126.9	53	53	3.0E-03	11	QuadMin	-128.8	60	56	1.0E-03	2	
<b>Inflection Point</b>						<b>Inflection Point</b>						
Mean	-201	102	98	2.0E-03	9	Mean	-237.2	114	64	4.0E-03	9	
Max	-210.1	105	95	1.0E-03	3	Max	-240.6	120	93	1.0E-03	1	
Min	-199.1	100	100	2.0E-03	6	Min	-241.2	112	38	1.0E-03	3	
QuadMean	-215.5	102	94	3.0E-03	6	QuadMean	-243.9	117	14	2.0E-03	4	
<b>QuadMax</b>	<b>-230.4</b>	<b>105</b>	<b>94</b>	<b>2.0E-03</b>	<b>2</b>	QuadMax	-240.1	120	93	3.0E-03	1	
QuadMin	-213	101	101	1.0E-03	3	<b>QuadMin</b>	<b>-271.9</b>	<b>109</b>	<b>37</b>	<b>6.0E-03</b>	<b>1</b>	
<b>Growth Rate</b>						<b>Growth Rate</b>						
Mean	-298	102	94	2.0E-03	6	Mean	-403.4	120	5	2.0E-03	3	
Max	-317.1	105	95	1.0E-03	2	Max	-348.5	120	88	1.0E-03	1	
Min	-296.1	100	100	1.0E-03	3	Min	-451.8	112	37	1.0E-03	1	

QuadMean	-328.1	102	93	2.0E-03	4	QuadMean	-410.1	120	3	2.0E-03	2
<b>QuadMax</b>	<b>-357.2</b>	<b>118</b>	<b>94</b>	<b>4.0E-03</b>	<b>1</b>	QuadMax	-350.8	120	88	1.0E-03	1
QuadMin	-319.2	101	101	2.0E-03	4	<b>QuadMin</b>	<b>-486.5</b>	<b>109</b>	<b>37</b>	<b>2.0E-03</b>	<b>1</b>
<b>FedAlpha</b>	<b>SST</b>					<b>FedAlpha</b>	<b>Air Temperature</b>				
<b>Asymptote</b>						<b>Asymptote</b>					
Model	$\Delta$ AIC	BestModel Open	BestModel Close	Pc	%Confidence	Model	$\Delta$ AIC	BestModel Open	BestModel Close	Pc	%Confidence
Mean	-34.93	93	0	9.0E-03	24	Mean	-27.1709	36	36	2.5E-02	35
Max	-32.64	78	37	2.8E-02	38	Max	-28.3004	94	64	3.2E-02	38
Min	-33.56	74	16	3.0E-03	12	Min	-30.9086	36	32	2.0E-03	5
<b>QuadMean</b>	<b>-35.7</b>	<b>91</b>	<b>0</b>	<b>1.2E-02</b>	<b>20</b>	QuadMean	-29.6257	25	24	2.1E-02	26
QuadMax	-34.25	68	37	4.1E-02	35	QuadMax	-32.0408	26	24	5.6E-02	32
QuadMin	-33.18	52	52	5.0E-03	14	QuadMin	-33.645	36	21	3.0E-03	5
<b>Inflection Point</b>						<b>Inflection Point</b>					
Mean	-90.27	118	0	3.0E-03	11	Mean	-105.764	120	0	6.0E-03	19
Max	-81.78	84	75	5.0E-03	17	Max	-85.5132	80	12	6.0E-03	18
Min	-94.55	94	0	2.0E-03	5	Min	-100.035	118	72	3.0E-03	11
QuadMean	-124.7	96	3	2.0E-03	6	QuadMean	-120.085	82	0	3.0E-03	7
<b>QuadMax</b>	<b>-134.3</b>	<b>120</b>	<b>24</b>	<b>3.0E-03</b>	<b>4</b>	QuadMax	-99.1459	80	15	1.3E-02	13
QuadMin	-100.1	52	51	2.0E-03	5	QuadMin	-112.194	118	0	6.0E-03	14
<b>Growth Rate</b>						<b>Growth Rate</b>					
Mean	-37.42	95	92	9.0E-03	24	Mean	-41.7106	119	118	1.1E-02	27
Max	-37.99	95	93	3.0E-03	10	Max	-42.9959	119	118	2.0E-03	3
Min	-42.8	96	13	1.5E-02	27	Min	-49.5519	118	72	2.0E-03	7
<b>QuadMean</b>	<b>-43.16</b>	<b>85</b>	<b>30</b>	<b>1.5E-02</b>	<b>27</b>	QuadMean	-40.3146	120	65	6.0E-02	7
QuadMax	-41.66	61	61	1.6E-02	27	QuadMax	-41.0167	119	118	9.0E-03	10
QuadMin	-42.73	82	33	3.5E-02	32	QuadMin	-50.7467	118	72	5.0E-03	10

**Appendix A Table A10:** Results from a linear model with of sea-surface temperature with a categorical year fit as a predictor. The estimate for each year is show relative to the first year of the analysis (1998). Standard error and 95% highest posterior density intervals are shown. Years with 95% confidence intervals that did not overlap zero are shown.

Term	SST Estimate	Std.error	95% HPD
b_Intercept (1998)	<b>10.18</b>	<b>0.27</b>	<b>9.67, 10.69</b>
b_Year1999	-0.65	0.37	-1.37, 0.08
b_Year2000	0.10	0.37	-0.63, 0.83
b_Year2001	-0.37	0.36	-1.09, 0.33
b_Year2002	-0.62	0.37	-1.44, 0.03
b_Year2003	0.41	0.37	-0.30, 1.17
b_Year2004	0.70	0.37	-0.05, 1.43
b_Year2005	<b>1.22</b>	<b>0.38</b>	<b>0.50, 1.96</b>
b_Year2006	-0.04	0.38	-0.77, 0.71
b_Year2007	<b>-0.90</b>	<b>0.38</b>	<b>-1.59, -0.13</b>
b_Year2008	<b>-1.39</b>	<b>0.37</b>	<b>-2.12, -0.65</b>
b_Year2009	-0.61	0.38	-1.34, 0.16
b_Year2010	-0.49	0.38	-1.19, 0.32
b_Year2011	-0.33	0.38	-1.09, 0.39
b_Year2012	<b>-1.44</b>	<b>0.37</b>	<b>-2.15, -0.67</b>
b_Year2013	0.02	0.38	-0.69, 0.78
b_Year2014	0.14	0.38	-0.61, 0.84
b_Year2015	<b>1.07</b>	<b>0.38</b>	<b>0.32, 1.81</b>
b_Year2016	<b>1.71</b>	<b>0.37</b>	<b>1.02, 2.50</b>
b_Year2017	0.16	0.37	-0.58, 0.88
b_Year2018	-0.29	0.37	-1.08, 0.42
sigma	<b>3.24</b>	<b>0.04</b>	<b>3.17, 3.32</b>

**Appendix A Table A11:** Results from a linear model with of air temperature with a categorical year fit as a predictor. The estimate for each year is show relative to the first year of the analysis (1998). Standard error and 95% highest posterior density intervals are shown. Years with 95% confidence intervals that did not overlap zero are shown.

Term	Air Temp Estimate	Std.error	95% HPD
<b>b_Intercept</b>	<b>9.13</b>	<b>0.28</b>	<b>8.61, 9.72</b>
b_Year1999	-0.62	0.41	-1.36, 0.27
<b>b_Year2000</b>	<b>-0.83</b>	<b>0.41</b>	<b>-1.60, -0.02</b>
b_Year2001	-0.29	0.42	-1.04, 0.60
b_Year2002	-0.42	0.40	-1.22, 0.34
b_Year2003	0.27	0.41	-0.52, 1.04
<b>b_Year2004</b>	<b>1.21</b>	<b>0.41</b>	<b>0.40, 1.99</b>
<b>b_Year2005</b>	<b>2.65</b>	<b>0.41</b>	<b>1.85, 3.47</b>
b_Year2006	0.22	0.41	-0.54, 1.07
b_Year2007	-0.05	0.41	-0.87, 0.75
b_Year2008	-1.21	0.40	-1.99, -0.42
b_Year2009	-0.28	0.40	-1.03, 0.54
b_Year2010	-0.45	0.41	-1.24, 0.36
b_Year2011	0.08	0.41	-0.72, 0.90
b_Year2012	-0.80	0.41	-1.58, 0.00
b_Year2013	-0.13	0.40	-0.90, 0.68
b_Year2014	0.56	0.40	-0.24, 1.32
<b>b_Year2015</b>	<b>1.73</b>	<b>0.42</b>	<b>0.90, 2.55</b>
<b>b_Year2016</b>	<b>1.93</b>	<b>0.41</b>	<b>1.12, 2.72</b>
b_Year2017	0.22	0.42	-0.58, 1.04
b_Year2018	-0.01	0.40	-0.80, 0.78
sigma	3.61	0.05	3.52, 3.70

**Appendix A Table A12:** Full environmental model for **unfed alpha nestlings**. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2 and the effect of an interaction between two windows is indicated with a colon. For example, the term A\_A1WINTEMP:A1WINSST would indicate the effect of an interaction on the asymptote between the asymptote window for air temperature and the asymptote window for sea-surface temperature.

<b>Group-Level Effects:</b>							
<b>~ChickID (Number of levels: 1190)</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sd(A_Intercept)	0.36	0.01	0.34	0.39	1	2937	4749
sd(k_Intercept)	0.44	0.02	0.39	0.49	1	2797	6259
sd(T_Intercept)	1.96	0.07	1.83	2.09	1	2657	5214
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.09</b>	<b>0.07</b>	<b>-0.04</b>	<b>0.23</b>	<b>1</b>	<b>3290</b>	<b>5728</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.09</b>	<b>0.04</b>	<b>0.01</b>	<b>0.18</b>	<b>1</b>	<b>2041</b>	<b>4477</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.96</b>	<b>0.02</b>	<b>-0.99</b>	<b>-0.93</b>	<b>1</b>	<b>502</b>	<b>1487</b>
<b>~Year (Number of levels: 21)</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sd(A_Intercept)	0.19	0.04	0.12	0.29	1	2752	4225
sd(k_Intercept)	0.49	0.08	0.36	0.69	1	4079	5878
sd(T_Intercept)	1.35	0.23	0.97	1.88	1	3741	6032
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.61</b>	<b>0.17</b>	<b>0.22</b>	<b>0.87</b>	<b>1</b>	<b>2797</b>	<b>4472</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>-0.57</b>	<b>0.18</b>	<b>-0.85</b>	<b>-0.16</b>	<b>1</b>	<b>2493</b>	<b>4313</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.91</b>	<b>0.05</b>	<b>-0.97</b>	<b>-0.77</b>	<b>1</b>	<b>4851</b>	<b>6916</b>
<b>Population-Level Effects:</b>							
	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
d_Intercept	2.07	0.04	2	2.14	1	8149	9402
A_Intercept	3.71	0.65	2.42	4.97	1	6109	7904
<b>A_A1WINTEMP</b>	<b>2.27</b>	<b>0.97</b>	<b>0.35</b>	<b>4.17</b>	<b>1</b>	<b>3158</b>	<b>8332</b>
<b>A_A1WINSST</b>	<b>1.18</b>	<b>1.09</b>	<b>-0.93</b>	<b>3.31</b>	<b>1</b>	<b>5168</b>	<b>7372</b>
<b>A_IA1WINSSTE2</b>	<b>-1.3</b>	<b>0.52</b>	<b>-2.31</b>	<b>-0.31</b>	<b>1</b>	<b>4617</b>	<b>6866</b>
<b>A_A1WINTEMP:A1WINSST</b>	<b>1.86</b>	<b>0.93</b>	<b>0</b>	<b>3.69</b>	<b>1</b>	<b>1593</b>	<b>9183</b>
A_A1WINTEMP:IA1WINSSTE2	1.25	0.92	-0.52	3.07	1	8079	7825
k_Intercept	4.37	0.66	3.11	5.69	1	8210	7767
k_A1WINSST	0.91	1.12	-1.33	3.05	1	6823	7595
k_IA1WINSSTE2	-0.65	0.51	-1.64	0.34	1	6425	8103
T_Intercept	13.59	0.32	12.97	14.22	1	4070	4936
<b>Family Specific Parameters:</b>							
	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95%CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sigma	20.62	0.19	20.3	21.0	1	8220	9531

**Appendix A Table A13: Full environmental model for unfed beta nestlings.** The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with an additional prefix after an underscore that indicates which parameter the window was originally identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2 and the effect of an interaction between two windows is indicated with a colon. For example, the term A\_A1WINTEMP:A1WINSST would indicate the estimated effect of an interaction on the asymptote between the asymptote window for air temperature and the asymptote window for sea-surface temperature identified in the sliding window analysis.

<b>Group-Level Effects:</b>							
<b>~ChickID (Number of levels: 788)</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sd(A_Intercept)	0.43	0.02	0.38	0.47	1	2863	5058
sd(k_Intercept)	0.53	0.04	0.45	0.6	1	4058	6526
sd(T_Intercept)	1.95	0.11	1.75	2.18	1	2550	4264
<b>cor(A_Intercept,k_Intercept)</b>	<b>-0.14</b>	<b>0.09</b>	<b>-0.32</b>	<b>0.05</b>	<b>1</b>	<b>3324</b>	<b>5667</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.47</b>	<b>0.06</b>	<b>0.36</b>	<b>0.57</b>	<b>1</b>	<b>2754</b>	<b>4880</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.92</b>	<b>0.03</b>	<b>-0.97</b>	<b>-0.85</b>	<b>1</b>	<b>2205</b>	<b>4632</b>
<b>~Year (Number of levels: 21)</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sd(A_Intercept)	0.39	0.09	0.24	0.61	1	3919	5803
sd(k_Intercept)	0.41	0.11	0.23	0.66	1	3461	5942
sd(T_Intercept)	1.1	0.31	0.59	1.81	1	2569	4518
<b>cor(A_Intercept,k_Intercept)</b>	<b>-0.04</b>	<b>0.29</b>	<b>-0.59</b>	<b>0.52</b>	<b>1</b>	<b>3822</b>	<b>5603</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.51</b>	<b>0.23</b>	<b>-0.03</b>	<b>0.86</b>	<b>1</b>	<b>4170</b>	<b>5937</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.61</b>	<b>0.22</b>	<b>-0.91</b>	<b>-0.09</b>	<b>1</b>	<b>3862</b>	<b>6347</b>
<b>Population-Level Effects:</b>							
	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
d_Intercept	1.95	0.06	1.84	2.06	1	16707	6479
A_Intercept	3.56	0.88	1.82	5.27	1	14698	7313
A_A1WINSST	0.86	2.51	-4.01	5.82	1	6556	6804
A_IA1WINSSTE2	-0.26	1.48	-3.15	2.68	1	5992	6443
A_k1WINSST	2.08	2.75	-3.31	7.59	1	6285	6645
A_ik1WINSSTE2	-2.5	2.08	-6.66	1.6	1	6284	6698
<b>A_Ti1WINTEMP</b>	<b>-4.26</b>	<b>0.83</b>	<b>-5.89</b>	<b>-2.66</b>	<b>1</b>	<b>6631</b>	<b>7038</b>
<b>A_ITi1WINTEMPE2</b>	<b>-2.93</b>	<b>0.68</b>	<b>-4.26</b>	<b>-1.59</b>	<b>1</b>	<b>7000</b>	<b>7845</b>
<b>A_A1WINSST:Ti1WINTEMP</b>	<b>2.07</b>	<b>0.93</b>	<b>0.27</b>	<b>3.9</b>	<b>1</b>	<b>17001</b>	<b>7362</b>
A_k1WINSST:Ti1WINTEMP	1.77	0.9	-0.02	3.5	1	17915	7267
A_IA1WINSSTE2:Ti1WINTEMP	0.05	0.72	-1.35	1.47	1	10594	7960
A_ik1WINSSTE2:Ti1WINTEMP	0.52	0.75	-0.96	1.99	1	11781	7313
A_IA1WINSSTE2:ITi1WINTEMPE2	0.79	0.69	-0.54	2.15	1	8489	7567
A_ik1WINSSTE2:ITi1WINTEMPE2	1.26	0.74	-0.18	2.74	1	12148	7829

k_Intercept	5.02	0.68	3.69	6.34	1	9389	7701
k_k1WIN	0.63	1.95	-3.22	4.47	1	8042	6911
k_lk1WINE2	-1.88	1.55	-4.91	1.24	1	7074	6888
<b>k_Ti1WINTEMP</b>	<b>-2.9</b>	<b>0.52</b>	<b>-3.91</b>	<b>-1.88</b>	<b>1</b>	<b>9700</b>	<b>7939</b>
<b>k_k1WINSST:Ti1WINTEMP</b>	<b>2.42</b>	<b>0.8</b>	<b>0.86</b>	<b>4</b>	<b>1</b>	<b>14919</b>	<b>6562</b>
k_lk1WINSSTE2:Ti1WINTEMP	1.08	0.63	-0.15	2.31	1	14703	8143
T_Intercept	13.17	1.35	10.59	15.9	1	8883	7248
T_k1WINSST	-4.84	3.58	-12.38	1.76	1	8602	6634
<b>T_lk1WINSSTE2</b>	<b>6.23</b>	<b>2.96</b>	<b>0.67</b>	<b>12.45</b>	<b>1</b>	<b>6591</b>	<b>6711</b>
<b>Family Specific Parameters:</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sigma	19.74	0.28	19.2	20.29	1	8977	7593

**Appendix A Table A14: Full environmental model for fed alpha nestlings.** The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with an additional prefix after an underscore that indicates which parameter the window was originally identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2 and the effect of an interaction between two windows is indicated with a colon. For example, the term A\_A1WINTEMP:A1WINSST would indicate the estimated effect of an interaction on the asymptote between the asymptote window for air temperature and the asymptote window for sea-surface temperature identified in the sliding window analysis.

Group-Level	Effects:						
~ChickID (Number of levels: 989)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.33	0.01	0.31	0.35	1	2253	4542
sd(k_Intercept)	0.46	0.03	0.41	0.52	1	528	1260
sd(T_Intercept)	2.2	0.07	2.06	2.35	1	1584	3249
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.09</b>	<b>0.08</b>	<b>-0.06</b>	<b>0.23</b>	<b>1</b>	<b>725</b>	<b>1239</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.08</b>	<b>0.05</b>	<b>-0.01</b>	<b>0.16</b>	<b>1</b>	<b>966</b>	<b>2031</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.96</b>	<b>0.02</b>	<b>-0.99</b>	<b>-0.92</b>	<b>1.01</b>	<b>270</b>	<b>806</b>
~Year (Number of levels: 20)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.05	0.03	0	0.1	1	527	1357
sd(k_Intercept)	0.21	0.05	0.13	0.31	1	3470	6130
sd(T_Intercept)	0.66	0.15	0.4	1	1	2261	4331
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.18</b>	<b>0.36</b>	<b>-0.56</b>	<b>0.81</b>	<b>1</b>	<b>1075</b>	<b>1755</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>-0.08</b>	<b>0.37</b>	<b>-0.78</b>	<b>0.62</b>	<b>1</b>	<b>815</b>	<b>1116</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.71</b>	<b>0.16</b>	<b>-0.93</b>	<b>-0.3</b>	<b>1</b>	<b>3051</b>	<b>5289</b>
Population-Level	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.27	0.04	2.2	2.34	1	14853	7526
A_Intercept	4.05	0.67	2.72	5.35	1	2947	5301
A_A1WINTEMP	1.47	0.94	-0.41	3.27	1	2469	4601
A_IA1WINTEMPE2	-0.7	0.4	-1.48	0.1	1	2285	4123
A_Ti1WINTEMP	0.03	0.17	-0.32	0.35	1	1643	2842
A_k1WINTEMP	-0.7	1.3	-3.21	1.85	1	2309	4046
A_ik1WINTEMPE2	0.2	0.48	-0.76	1.12	1	2319	3641
k_Intercept	4.65	0.77	3.14	6.19	1	8898	7603
k_A1WINTEMP	1.85	1.52	-1.22	4.75	1	3718	5521
k_IA1WINTEMPE2	-0.83	0.67	-2.12	0.5	1	3224	5515
k_Ti1WINTEMP	-0.56	0.37	-1.29	0.17	1	4087	6176
k_k1WINTEMP	0.23	1.75	-3.12	3.73	1	3803	5984
k_ik1WINTEMPE2	-0.37	0.65	-1.66	0.88	1	3551	5327
T_Intercept	14.12	1.72	10.76	17.51	1	8810	7655
T_A1WINTEMP	-1.79	3.28	-8.26	4.6	1	3727	5315

T_IA1WINTEMPE2	0.5	1.52	-2.43	3.55	1	2931	5058
T_Ti1WINTEMP	<b>2.55</b>	<b>1.17</b>	<b>0.31</b>	<b>4.86</b>	<b>1</b>	<b>2874</b>	<b>4848</b>
T_k1WINTEMP	-2.79	3.32	-9.39	3.69	1	4296	5753
T_Ik1WINTEMPE2	1.41	1.31	-1.12	4.04	1	3571	5685

**Appendix A Table A15: Full environmental model for unfed alpha nestlings with beta overlap.** The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with an additional prefix after an underscore that indicates which parameter the window was originally identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2 and the effect of an interaction between two windows is indicated with a colon. For example, the term A\_A1WINTEMP:A1WINSST would indicate the estimated effect of an interaction on the asymptote between the asymptote window for air temperature and the asymptote window for sea-surface temperature identified in the sliding window analysis.

Group-Level	Effects:						
~ChickID (Number of levels: 1191)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.35	0.01	0.33	0.38	1	2911	5136
sd(k_Intercept)	0.43	0.03	0.38	0.48	1	2162	4048
sd(T_Intercept)	1.89	0.07	1.77	2.03	1	2135	4125
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.09</b>	<b>0.07</b>	<b>-0.05</b>	<b>0.23</b>	<b>1</b>	<b>2368</b>	<b>4846</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.12</b>	<b>0.04</b>	<b>0.03</b>	<b>0.2</b>	<b>1</b>	<b>1760</b>	<b>3440</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.96</b>	<b>0.02</b>	<b>-0.99</b>	<b>-0.92</b>	<b>1.01</b>	<b>460</b>	<b>1161</b>
~Year (Number of levels: 21)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.13	0.03	0.08	0.2	1	2113	3493
sd(k_Intercept)	0.5	0.09	0.36	0.7	1	3230	4926
sd(T_Intercept)	1.05	0.2	0.73	1.5	1	3001	4517
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.4</b>	<b>0.23</b>	<b>-0.1</b>	<b>0.79</b>	<b>1</b>	<b>1526</b>	<b>2811</b>
cor(A_Intercept, T_Intercept)	-0.36	0.24	-0.78	0.14	1	1564	2560
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.84</b>	<b>0.09</b>	<b>-0.95</b>	<b>-0.61</b>	<b>1</b>	<b>3808</b>	<b>6286</b>
Population-Level	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.13	0.04	2.05	2.2	1	16843	6472
A_Intercept	5.51	0.26	5	6.03	1	2569	4992
A_BetaOverlap	0	0.01	-0.01	0.02	1	1890	3586
<b>A_A1WIN</b>	<b>-1.71</b>	<b>0.64</b>	<b>-2.95</b>	<b>-0.44</b>	<b>1</b>	<b>6577</b>	<b>5976</b>
A_A1WINTEMP	-0.14	5.63	-11.6	10.96	1	11156	6801
<b>A_A1WIN:A1WINTEMP</b>	<b>3.63</b>	<b>0.98</b>	<b>1.69</b>	<b>5.54</b>	<b>1</b>	<b>17740</b>	<b>7842</b>
<b>A_BetaOverlap:A1WIN</b>	<b>-0.36</b>	<b>0.1</b>	<b>-0.56</b>	<b>-0.17</b>	<b>1</b>	<b>9879</b>	<b>7834</b>
<b>A_BetaOverlap:A1WINTEMP</b>	<b>3.56</b>	<b>0.99</b>	<b>1.64</b>	<b>5.5</b>	<b>1</b>	<b>10021</b>	<b>7191</b>
k_Intercept	4.44	0.12	4.21	4.67	1	3358	5176
<b>k_BetaOverlap</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0.01</b>	<b>1</b>	<b>5048</b>	<b>7473</b>
T_Intercept	13.97	0.98	12.08	15.92	1	6267	7388
T_BetaOverlap	0.01	0.02	-0.03	0.06	1	4117	6295
T_Ti1WIN	-1.31	3.85	-8.86	6.33	1	11437	7264
T_ITi1WINE2	-5.6	4.31	-14.24	2.7	1	10857	7583
T_Ti1WINTEMP	-1.28	3.83	-9.04	6.16	1	10589	7013

T_ITi1WINTEMPE2	-5.6	4.34	-14.45	2.76	1	11268	7152
T_BetaOverlap:Ti1WIN	-0.01	1.43	-2.79	2.74	1	9255	7437
T_BetaOverlap:Ti1WINTEMP	-0.05	1.43	-2.78	2.73	1	9245	7532
T_Ti1WIN:Ti1WINTEMP	14.24	1.93	10.45	18.03	1	19259	7580

Family	Specific	Parameters:				Rhat	Bulk_ESS	Tail_ESS
	Estimate	Est.Error	l-95%CI	u-95%CI				
sigma	20.59	0.19	20.22	20.97	1	6857	7770	

**Appendix A Table A16: Full environmental model for fed alpha nestlings with beta overlap.**

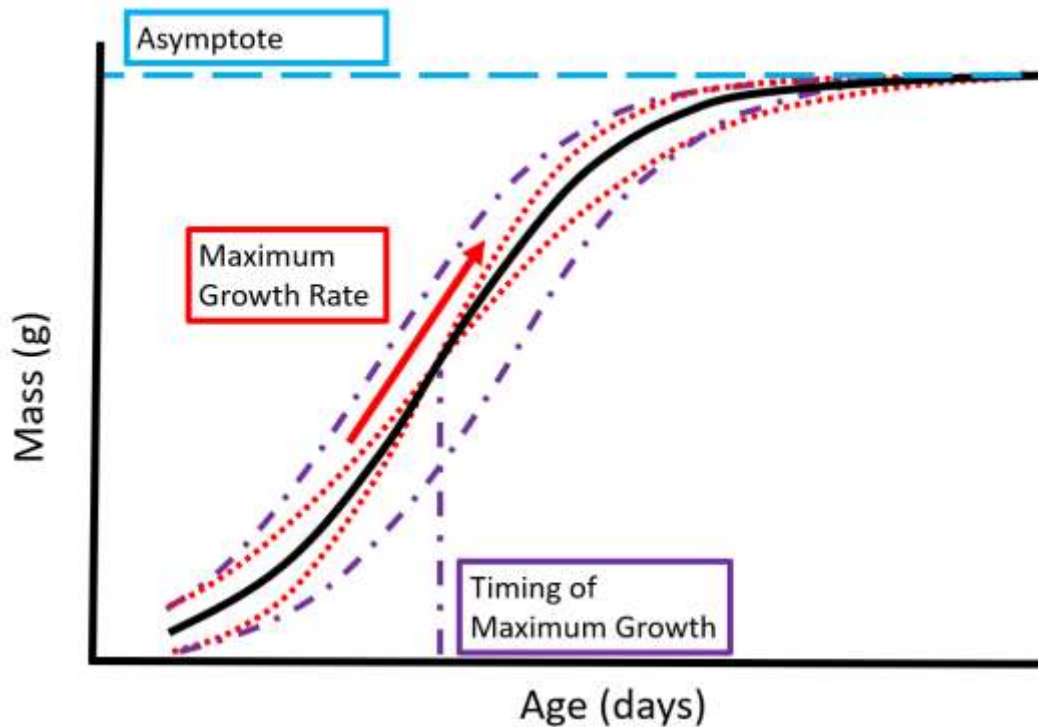
The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with an additional prefix after an underscore that indicates which parameter the window was originally identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2 and the effect of an interaction between two windows is indicated with a colon. For example, the term A\_A1WINTEMP:A1WINSST would indicate the estimated effect of an interaction on the asymptote between the asymptote window for air temperature and the asymptote window for sea-surface temperature identified in the sliding window analysis.

Group-Level	Effects:						
~ChickID (Number of levels: 989)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.32	0.01	0.3	0.34	1	2228	4671
sd(k_Intercept)	0.45	0.03	0.4	0.51	1	511	1600
sd(T_Intercept)	2.11	0.07	1.98	2.25	1	1388	3278
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.06</b>	<b>0.08</b>	<b>-0.1</b>	<b>0.21</b>	<b>1</b>	<b>792</b>	<b>2044</b>
<b>cor(A_Intercept, T_Intercept)</b>	<b>0.12</b>	<b>0.05</b>	<b>0.03</b>	<b>0.2</b>	<b>1</b>	<b>1166</b>	<b>1800</b>
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.96</b>	<b>0.02</b>	<b>-0.99</b>	<b>-0.92</b>	<b>1</b>	<b>214</b>	<b>957</b>
~Year (Number of levels: 20)	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.09	0.02	0.04	0.14	1	1474	1118
sd(k_Intercept)	0.24	0.05	0.16	0.36	1	3831	6372
sd(T_Intercept)	0.73	0.16	0.47	1.09	1	2501	4786
<b>cor(A_Intercept,k_Intercept)</b>	<b>0.14</b>	<b>0.29</b>	<b>-0.44</b>	<b>0.66</b>	<b>1</b>	<b>1708</b>	<b>3243</b>
cor(A_Intercept, T_Intercept)	-0.13	0.28	-0.65	0.44	1	1639	2966
<b>cor(k_Intercept, T_Intercept)</b>	<b>-0.7</b>	<b>0.17</b>	<b>-0.92</b>	<b>-0.29</b>	<b>1</b>	<b>3593</b>	<b>5488</b>
Population-Level	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.29	0.04	2.22	2.37	1	16772	7864
A_Intercept	4.4	0.68	3.07	5.73	1	4701	6100
A_BetaOverlap	-0.01	0.03	-0.07	0.05	1	2619	4421
A_Ti1WIN	-3.13	1.84	-6.74	0.48	1	2077	3879
A_ITi1WINE2	1.17	0.66	-0.12	2.48	1	2095	3691
<b>A_k1WIN</b>	<b>4.19</b>	<b>1.83</b>	<b>0.61</b>	<b>7.77</b>	<b>1</b>	<b>1906</b>	<b>3236</b>
<b>A_ik1WINE2</b>	<b>-2.25</b>	<b>0.81</b>	<b>-3.83</b>	<b>-0.68</b>	<b>1</b>	<b>1949</b>	<b>3402</b>
A_BetaOverlap:Ti1WIN	-0.01	0.08	-0.17	0.15	1	1610	2869
A_BetaOverlap:ITi1WINE2	0	0.03	-0.06	0.06	1	1647	2870
A_BetaOverlap:k1WIN	0.02	0.08	-0.13	0.18	1	1600	2662
A_BetaOverlap:ik1WINE2	0	0.04	-0.08	0.07	1	1668	2853
k_Intercept	5.7	0.27	5.18	6.23	1	3516	5863
k_BetaOverlap	-0.02	0.01	-0.04	0	1	3336	5676
<b>k_k1WINTEMP</b>	<b>-0.86</b>	<b>0.25</b>	<b>-1.34</b>	<b>-0.39</b>	<b>1</b>	<b>3552</b>	<b>5566</b>
<b>k_BetaOverlap:k1WINTEMP</b>	<b>0.02</b>	<b>0.01</b>	<b>0</b>	<b>0.04</b>	<b>1</b>	<b>3377</b>	<b>5528</b>

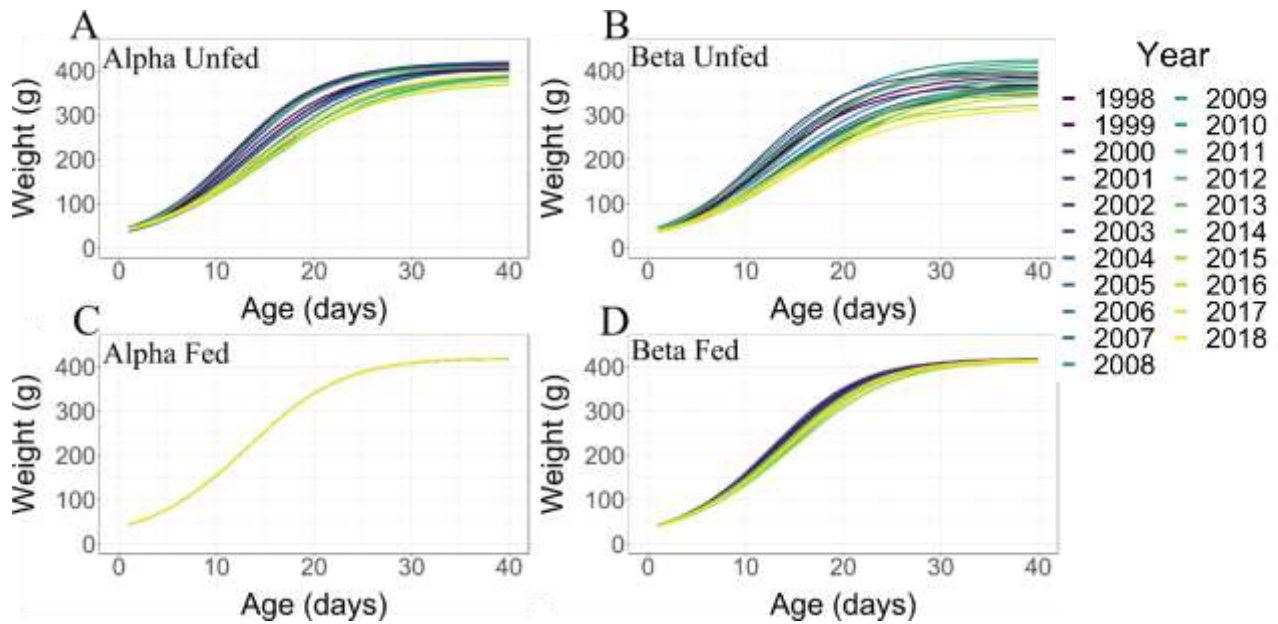
T_Intercept	14.23	1.65	10.98	17.5	1	6643	7308
T_BetaOverlap	-0.07	0.13	-0.33	0.19	1	3134	5016
<b>T_Ti1WINTEMP</b>	<b>-5.4</b>	<b>2.53</b>	<b>-10.38</b>	<b>-0.44</b>	<b>1</b>	<b>5175</b>	<b>6381</b>
T_ITi1WINTEMPE2	1.19	1.03	-0.79	3.23	1	5111	6491
<b>T_k1WINTEMP</b>	<b>4.44</b>	<b>1.09</b>	<b>2.27</b>	<b>6.59</b>	<b>1</b>	<b>3102</b>	<b>4297</b>
T_BetaOverlap:Ti1WINTEMP	0.19	0.19	-0.19	0.58	1	3183	4541
T_BetaOverlap:ITi1WINTEMPE2	-0.07	0.07	-0.21	0.08	1	3195	4778
T_BetaOverlap:k1WINTEMP	-0.09	0.05	-0.19	0.01	1	2581	4973
<b>Family</b>	<b>Specific</b>	<b>Parameters:</b>					
	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95%CI</b>	<b>u-95%CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
sigma	18.44	0.18	18.08	18.8	1	2748	6092

**Appendix A Table A17:** Correlations among selected predictors of nestling growth in final environmental models. For each predictor the prefix indicates which parameter the window was originally identified for in the sliding window analysis (A = Asymptote, Ti = Inflection point, k = Growth rate). Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST) or air temperature (TEMP). The final column indicates the Pearson’s correlation between each effect with the associated confidence intervals in brackets.

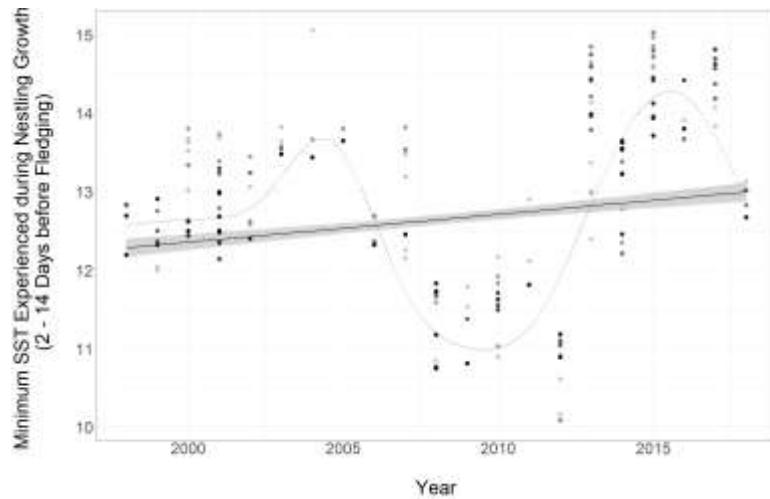
<b>Model</b>	<b>Predictors</b>	<b>Correlation</b>
<b>Unfed Alpha Nestlings</b>	A1WINSST, A1WINTEMP	0.74 [0.72, 0.77]
<b>Unfed Beta Nestlings</b>	A1WINSST, Ti1WINSST	0.82 [0.80, 0.84]
	A1WINSST, Ti1WINTEMP	0.32 [0.26, 0.38]
	Ti1WINSST, Ti1WINTEMP	0.45 [0.39, 0.50]
<b>Fed Alpha Nestlings</b>	Only one selected predictor	NA
<b>Fed Beta Nestlings</b>	No selected predictors in final model	NA
<b>Unfed Alpha Nestlings with Beta Overlap</b>	A1WINSST, A1WINTEMP	0.83 [0.81, 0.85]
<b>Fed Alpha nestlings with Beta Overlap</b>	k1WINSST, Ti1WINTEMP	0.84 [0.82, 0.85]
	k1WINSST, k1WINTEMP	0.53[0.48, 0.57]
	k1WINTEMP, Ti1WINTEMP	0.67 [0.64,0.71]



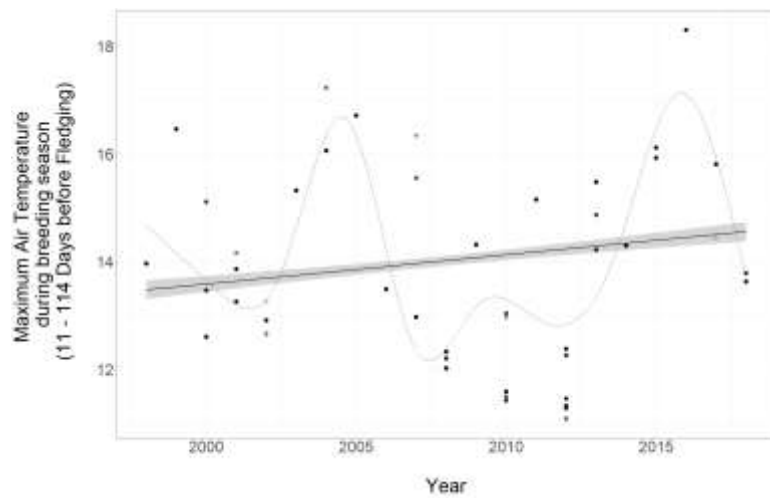
**Appendix A Figure A1:** Parameters of interest in our model of kittiwake growth. The maximum relative growth rate (red arrow) gives an indication of the speed of growth, the asymptote is an indication of the nestlings' maximum size (blue horizontal dash), and the timing of maximum growth is an indication of the age (in days) of when maximum growth occurs (purple/vertical dash + dotted line). Five growth curves are shown, with the same asymptote but varying in the timing of maximum growth (purple dash and dotted lines) or in maximum growth rate (red dotted lines). Figure is adapted from Sauve et al. 2021.



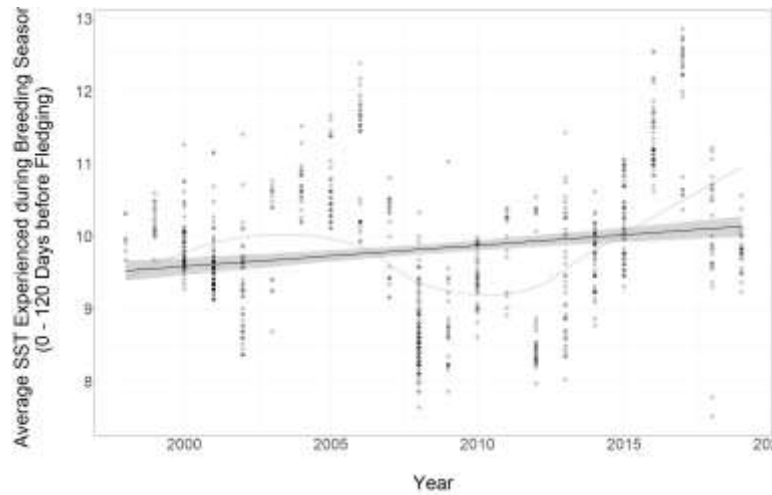
**Appendix A Figure A2:** Annual Unified Richards growth curves estimated from a random effect model with the intercept of the asymptote, maximum growth rate, and timing of maximum growth varying by year and individual. Estimates are plotted for each year of the study. Displayed are the growth curves for A) Alpha unfed kittiwakes, B) Beta unfed kittiwakes, C) Alpha fed kittiwakes, and D) Beta unfed kittiwakes. Points indicate individual weight measurements of nestlings. Points and loess curves are coloured by year of study.



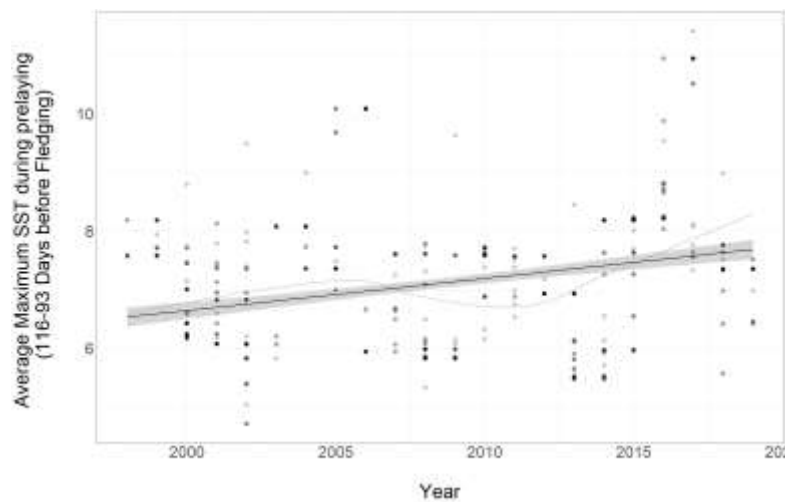
**Appendix A Figure A3:** Changes over time in the minimum sea-surface temperature window experienced by unfed alpha nestlings during nestling growth (2-14 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



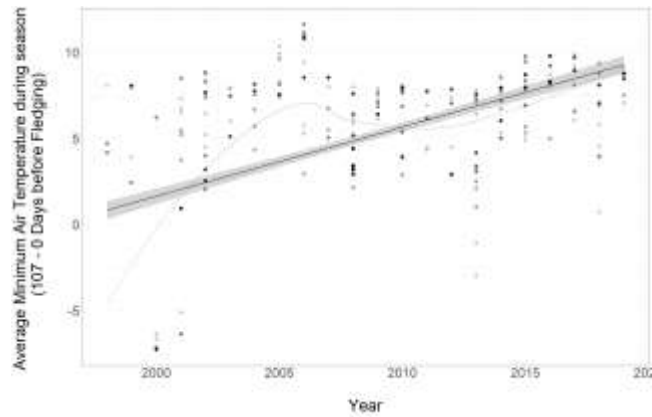
**Appendix A Figure A4:** Changes over time in the maximum air temperature experienced by unfed alpha nestlings during the breeding season (11-114 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



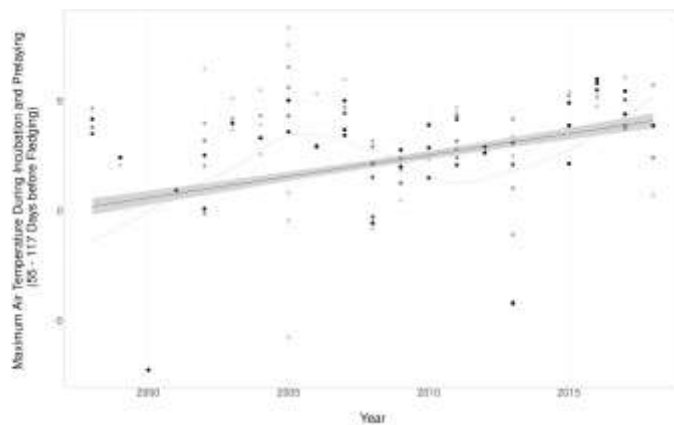
**Appendix A Figure A5:** Changes over time in the average sea-surface temperature experienced by unfed beta nestlings during the breeding season (0-120 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



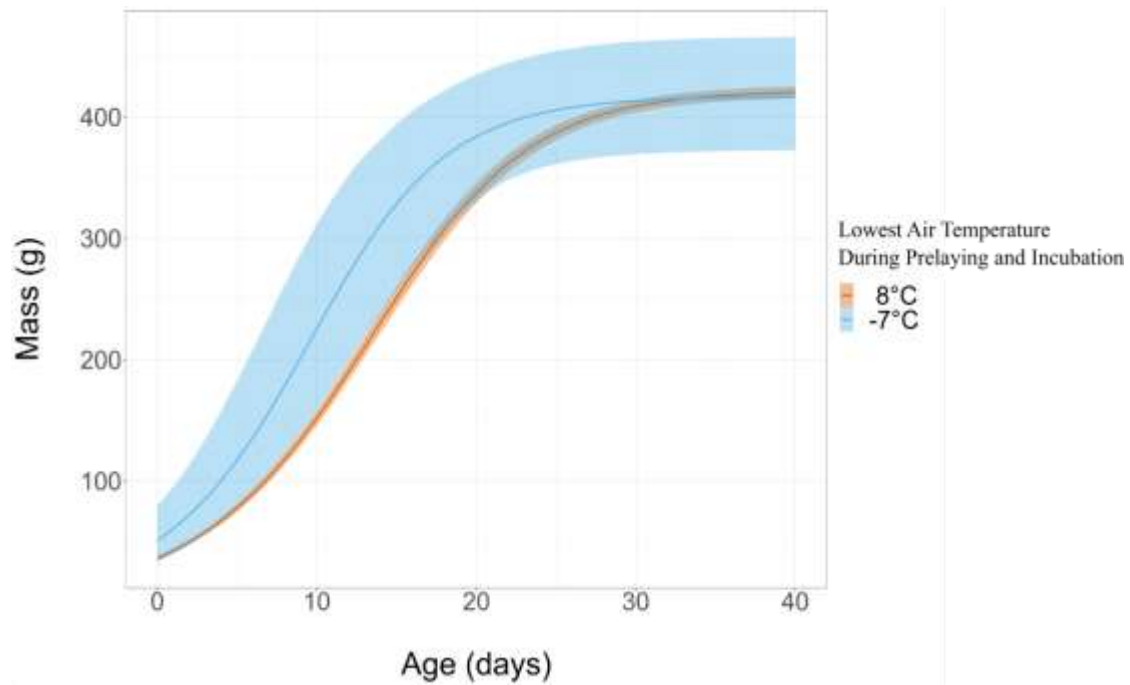
**Appendix A Figure A6:** Changes over time in the maximum sea-surface temperature experienced by unfed beta nestling's parents during the prelaying period (116-93 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



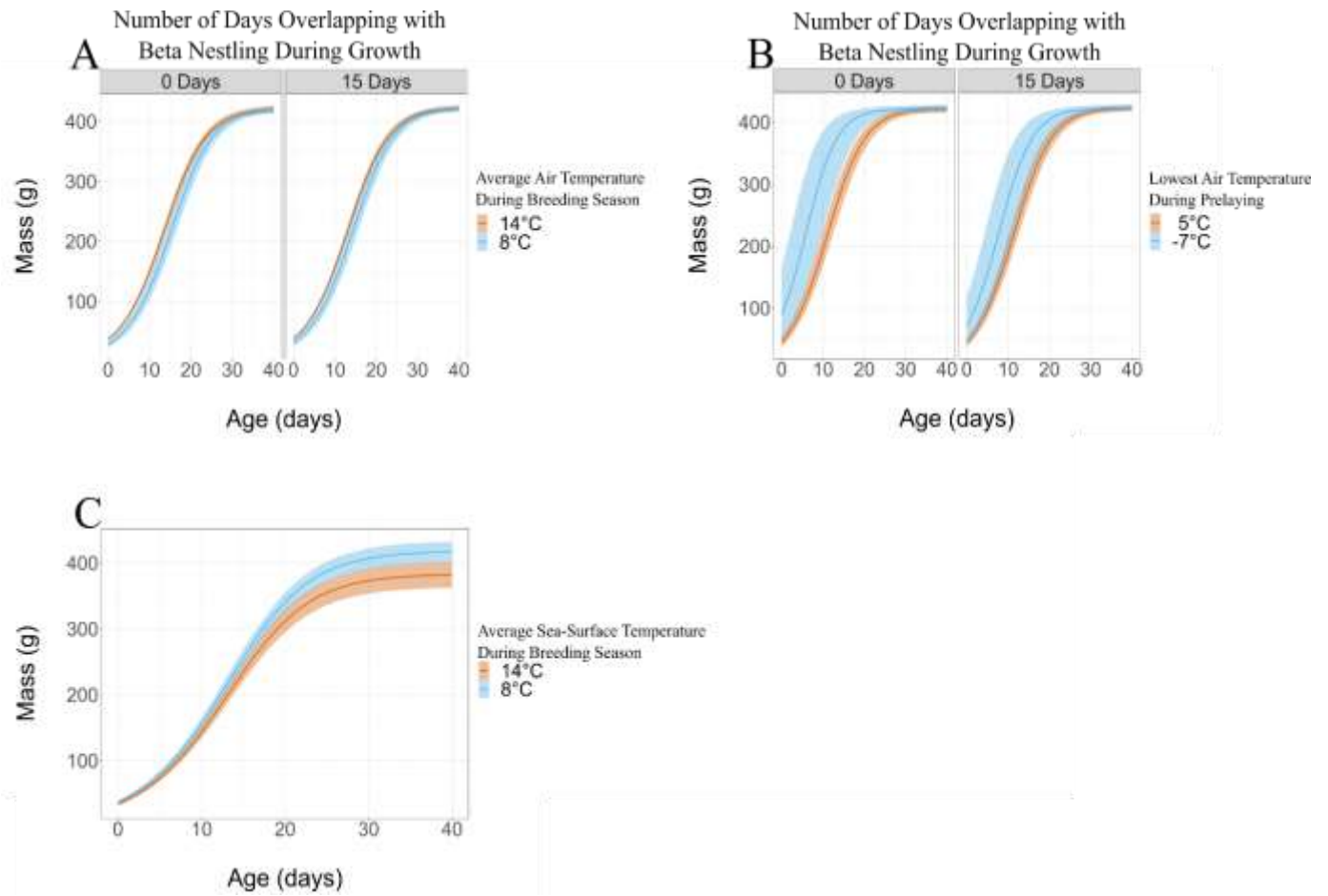
**Appendix A Figure A7:** Changes over time in the minimum air temperature experienced by unfed beta nestling during the breeding season (107-0 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



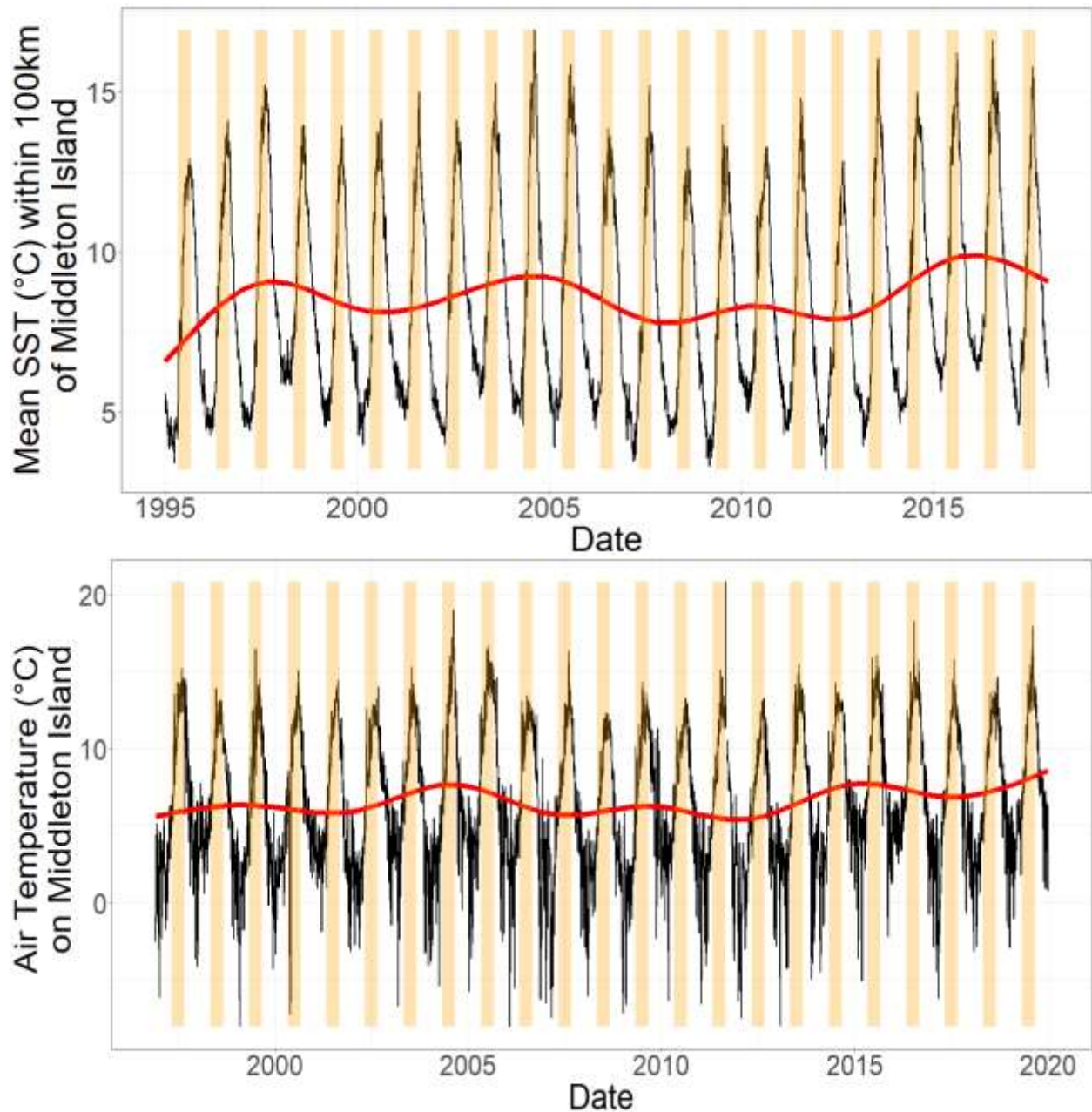
**Appendix A Figure A8:** Changes over time in the minimum air temperature experienced by fed beta nestling's parents during the prelying period and incubation (117-55 Days before fledging). Points indicate the temperature during this window relative to an individual nestling. Points are translucent and darker shades indicate a higher density of nestlings that experienced a particular temperature. The straight black line shows the linear trend over time and the thin grey line displays a non-linear loess fit.



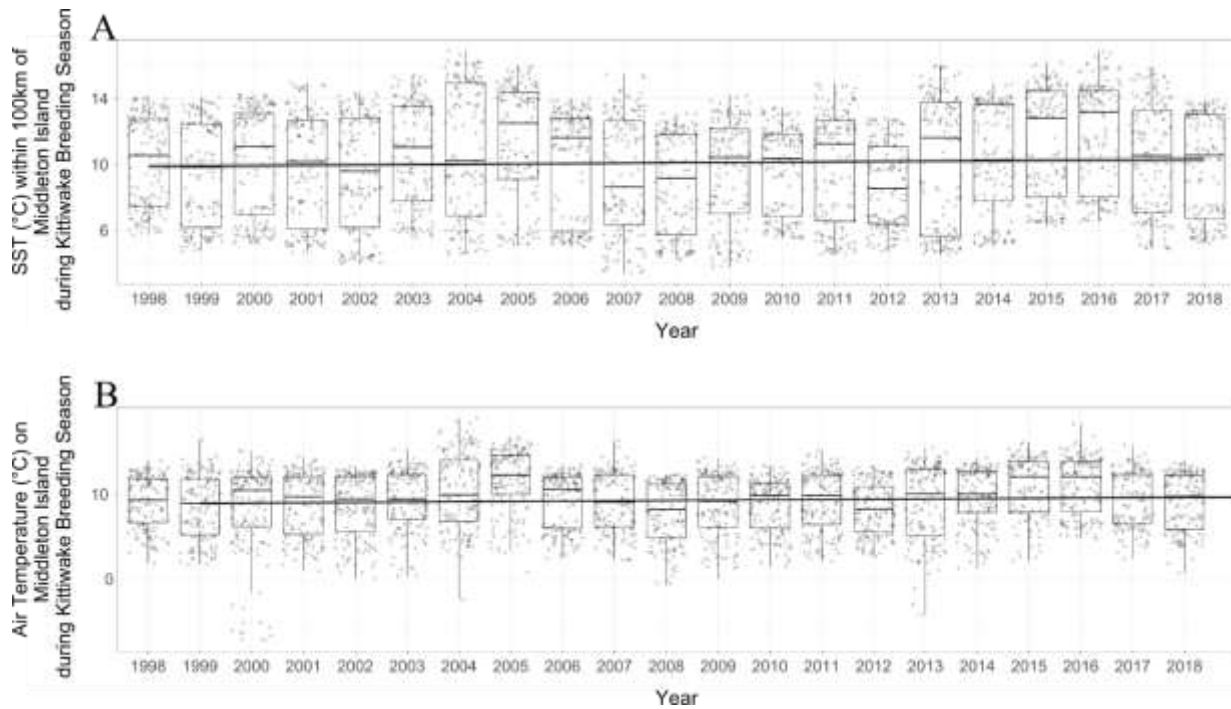
**Appendix A Figure A9:** Impacts of variation within the prelaying and incubation air temperature window on the growth of fed alpha nestlings. The extreme ranges of minimum air temperatures during this period are displayed.



**Appendix A Figure A10:** Interaction between the number of days a fed alpha nestling overlapped its growth with a younger sibling and a) the average air temperature in a season and b) the average sea-surface temperature of a season.



**Appendix A Figure A11:** Annual variation in sea-surface temperature and air temperature on Middleton Island. For A) sea-surface temperature and B) air temperature the daily variation follows the thin black line, a non-linear trend is displayed with the thick red line, and transparent orange rectangles highlight the time period within which we are searching for windows that predict nestling growth traits in this study.



**Appendix A Figure A12:** Annual variation in sea-surface temperature and air temperature on Middleton Island. For **A)** sea-surface temperature and **B)** air temperature a boxplot is displayed for each year showing the interquartile range, median, and the smallest or largest values within 1.5 times the interquartile range. Jittered grey points show the observed sea-surface or air temperatures for each year.

## **Appendix A References**

- Aldredge RA (2016). Using non-linear mixed effects models to identify patterns of chick growth in House Sparrows *Passer domesticus*. *Ibis* 158: 16–27. doi: 10.1111/ibi.12312
- Burnham KP, Anderson DR (1998). *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag. doi: 10.1007/978-1-4757-2917-7
- Roudybush TE, Grau CR, Petersen MR, Ainley DG, Hirsch KV, Gilman AP, Patten SM (1979) Yolk formation in some Charadriiform birds. *Condor* 81: 293–298. doi: 10.2307/1367636

## Appendix B Supplementary Material for Chapter 4

### APPENDIX B-I: DATA SUBSETS, MODEL OUTPUTS, & SLIDING WINDOW RESULTS

**Appendix B-I Table B1:** Details of the data subsets used to evaluate whether or not the different windows are identified between contemporary and historical periods in each dataset. For each species and location, the years included in an "historical" and "recent" data subset are reported, and the sample size (*n*) for the number of years and nestlings are reported for each subset.

Species	Colony Location	Total Sample Sizes	Years included in historical data subset	Years included in recent data subset
Black-legged Kittiwake	Middleton Island (Gulf of Alaska)	1998-2018 Years: 21 First-hatched nestlings: 1191 Second-hatched nestlings: 789	1998-2007 Years: 10 First-hatched nestlings: 534 Second-hatched nestlings: 333	2008- 2018 Years: 11 First-hatched nestlings: 657 Second-hatched nestlings: 456
Thick-billed Murre	Coats Island (Northern Hudson Bay)	1986-2010; 2017-2018 Years: 27 Nestlings: 1526	1986-1994 Years: 9 Nestlings: 454	1995-2010; 2017-2018 Years: 18 Nestlings: 1072
Glaucous-winged Gull	Middleton Island (Gulf of Alaska)	2002-2010; 2012; 2016-2018 Years: 13 Nestlings: 1558	2002-2008 Years: 7 Nestlings: 670	2009-2010; 2012; 2016-2018 Years: 6 Nestlings: 888

**Appendix B-I Table B2:** Growth model estimates and 95% credible intervals for kittiwake, gull, and murre chicks. Results are reported for the asymptote (A), maximum growth rate (k), timing of maximum growth (T), the shape parameter (d), and residual variance ( $\sigma$ ). The intercept and slope are reported for murre. Estimates of standard deviations (SD) are presented in square parentheses for variance components.

<b>Treatment</b>	<b>Rank</b>	<b>Population-Level Parameters</b>				
<b>Unfed</b>		<b>A</b>	<b>k</b>	<b>T</b>	<b>d</b>	<b><math>\sigma</math> (SD)</b>
<b>Black-legged Kittiwakes</b>	<b>First</b>	405 [397, 413]	4.49E-02 [4.28E-02, 4.72E-02]	13.5 [12.8, 14.1]	2.07 [1.99, 2.14]	20.6 [20.2, 21.0]
		N <sub>YEARS</sub> = 21 N <sub>IND</sub> = 1190				
	<b>Second</b>	379 [359, 399]	4.33E-02 [4.09E-02, 4.58E-02]	13.2 [12.5, 14.0]	1.90 [1.80, 2.00]	19.8 [19.3, 20.4]
		N <sub>YEARS</sub> = 21 N <sub>IND</sub> = 788				
<b>Glaucous-winged Gull</b>	<b>NA</b>	858 [812, 892]	4.69E-02 [4.46E-02, 4.95E-02]	16.0 [15.1, 16.9]	2.36 [2.22, 2.51]	34.2 [33.0, 35.3]
		N <sub>YEARS</sub> = 13 N <sub>IND</sub> = 1558				
<b>Thick-billed Murre</b>		<b>Intercept</b>	<b>Slope</b>	<b><math>\sigma</math> (SD)</b>		
	<b>NA</b>	68.8 [64.4, 73.4]	10.4 [10.0, 10.7]	12.3 [12.1, 12.6]		
		N <sub>YEARS</sub> = 27 N <sub>IND</sub> = 1528				
<b>Species</b>	<b>Annual Variation (SD)</b>			<b>Among Individual Variation (SD)</b>		
<b>Black-legged Kittiwakes</b>	<b>A</b>	<b>k</b>	<b>T</b>	<b>A</b>	<b>k</b>	<b>T</b>
<b>First</b>	16.5 [10.9, 24.2]	5.03E-03 [3.67E-03, 6.97E-03]	1.33 [0.952, 1.86]	36.2 [33.7, 38.4]	5.03E-03 [3.67E-03, 6.97E-02]	1.95 [1.83, 2.10]
<b>Second</b>	37.3 [23.9, 57.2]	4.84E-03 [3.22E-03, 7.03E-03]	1.48 [0.929, 2.25]	44.4 [40.2, 49.0]	5.37E-03 [3.72E-03, 6.12E-02]	1.97 [1.76, 2.19]
<b>Glaucous Winged Gull</b>	37.6 [2.97, 91.6]	2.91E-03 [1.40E-03, 5.20E-03]	1.24 [0.583, 2.28]	227 [210, 244]	6.77E-03 [5.96E-03, 7.60E-03]	3.73 [3.44, 4.05]
	<b>Intercept</b>	<b>Slope</b>		<b>Intercept</b>	<b>Slope</b>	

<b>Thick Billed Murre</b>	11.8[8.83, 15.9]	0.865 [0.605, 1.20]		9.00 [8.00, 9.96]	1.85 [1.73, 1.97]	
<b>Species or Rank</b>	<b>Annual Correlations</b>			<b>Among Individual Correlations</b>		
<b>Kittiwake First</b>	<b>A, k</b> 0.61 [0.22, 0.86]	<b>A, T</b> -0.48 [-0.81, 0.03]	<b>k, T</b> -0.92 [-0.98, -0.80]	<b>A, k</b> 0.10 [-0.03, 0.24]	<b>A, T</b> 0.09 [0.002, 0.18]	<b>k, T</b> -0.96 [-0.99, -0.93]
<b>Second</b>	0.31 [-0.18, 0.72]	-0.071 [-0.57, 0.44]	-0.87 [-0.97, -0.65]	-0.15 [-0.33, 0.04]	0.42 [0.30, 0.53]	-0.94 [-0.98, -0.89]
<b>Glaucous-winged Gull</b>	-0.18 [-0.86, 0.68]	-0.23 [-0.91, 0.62]	-0.25 [-0.79, 0.46]	-0.37 [-0.51, -0.22]	0.64 [0.59, 0.76]	-0.88 [-0.92, -0.83]
<b>Thick-billed Murre</b>	<b>Intercept, Slope</b>			<b>Intercept, Slope</b>		
	-0.23 [-0.59, 0.17]			-0.17 [-0.28, -0.05]		

**Appendix B-I Table B3:** Results from a linear model of thick-billed murres with a continuous linear and quadratic effect of year fit as a predictor for a model of linear growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

<b>Parameter Term</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>l-95% CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
Intercept	6.9E+01	6.8E-01	6.8E+01	7.0E+01	1.0E+00	5.7E+03	6.1E+03
<b>Age</b>	<b>1.0E+01</b>	<b>8.0E-02</b>	<b>9.9E+00</b>	<b>1.0E+01</b>	1.0E+00	5.6E+03	6.3E+03
<b>Year</b>	<b>8.2E-01</b>	<b>6.9E-02</b>	<b>6.8E-01</b>	<b>9.5E-01</b>	1.0E+00	4.3E+03	5.9E+03
<b>IYearE2</b>	<b>1.3E-02</b>	<b>6.3E-03</b>	<b>1.0E-04</b>	<b>2.5E-02</b>	1.0E+00	4.6E+03	5.6E+03
Age:Year	2.3E-03	8.2E-03	-1.4E-02	1.8E-02	1.0E+00	4.3E+03	5.8E+03
<b>Age:YearE2</b>	<b>2.4E-03</b>	<b>8.0E-04</b>	<b>9.0E-04</b>	<b>3.9E-03</b>	1.0E+00	4.9E+03	5.9E+03
sigma	2.1E+01	1.8E-01	2.1E+01	2.2E+01	1.0E+00	8.4E+03	6.7E+03

**Appendix B-I Table B4:** Results from a linear model of glaucous-winged gulls with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

<b>Parameter</b>	<b>1-95%</b>						
<b>Term</b>	<b>Estimate</b>	<b>Est.Error</b>	<b>CI</b>	<b>u-95% CI</b>	<b>Rhat</b>	<b>Bulk_ESS</b>	<b>Tail_ESS</b>
d_Intercept	1.9E+00	1.1E-01	1.7E+00	2.1E+00	1.0E+00	5.0E+03	5.6E+03
A_Intercept	9.6E+00	1.4E-01	9.3E+00	9.9E+00	1.0E+00	4.3E+03	5.0E+03
<b>A_Year2</b>	<b>-4.8E-02</b>	<b>1.3E-02</b>	<b>-7.3E-02</b>	<b>-2.4E-02</b>	1.0E+00	4.8E+03	5.4E+03
<b>A_IYear2E2</b>	<b>-1.9E-02</b>	<b>2.9E-03</b>	<b>-2.5E-02</b>	<b>-1.4E-02</b>	1.0E+00	4.1E+03	4.9E+03
k_Intercept	3.7E+00	1.1E-01	3.5E+00	3.9E+00	1.0E+00	4.6E+03	5.0E+03
k_Year2	2.1E-02	1.4E-02	-5.8E-03	4.9E-02	1.0E+00	5.4E+03	6.1E+03
<b>k_IYear2E2</b>	<b>1.5E-02</b>	<b>2.6E-03</b>	<b>9.9E-03</b>	<b>2.0E-02</b>	1.0E+00	5.7E+03	6.3E+03
Ti_Intercept	1.7E+01	3.4E-01	1.7E+01	1.8E+01	1.0E+00	5.4E+03	5.6E+03
Ti_Year2	1.4E-02	2.9E-02	-4.4E-02	7.0E-02	1.0E+00	4.7E+03	5.3E+03
<b>Ti_IYear2E2</b>	<b>-6.9E-02</b>	<b>6.2E-03</b>	<b>-8.1E-02</b>	<b>-5.7E-02</b>	1.0E+00	4.3E+03	5.2E+03

**Appendix B-I Table B5:** Results from a non-linear model of unfed alpha kittiwakes with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter. A prefix for each predictor is included to indicate which parameter the term corresponds to. The prefix *k* is used for the relative maximum growth rate, *d* for the shape of the growth curve (sigmoid when greater than 0), *T* for is the age at maximum growth, and *A* for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est.Error	l-95%CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	1.946	0.065	1.824	2.072	1	952	1065
A_Intercept	4.188	0.017	4.155	4.221	1	1051	989
<b>A_Year</b>	<b>-0.007</b>	0.002	<b>-0.01</b>	<b>-0.003</b>	1	1306	1534
<b>A_IYearE2</b>	<b>-0.002</b>	0	<b>-0.002</b>	<b>-0.001</b>	1	1343	1463
k_Intercept	4.537	0.057	4.42	4.649	1	1069	1158
<b>k_Year</b>	<b>-0.065</b>	0.007	<b>-0.078</b>	<b>-0.051</b>	1	1493	1390
k_IYearE2	0.001	0.001	-0.002	0.003	1	1275	1652
T_Intercept	12.387	0.177	12.031	12.724	1	1036	1171
<b>T_Year</b>	<b>0.119</b>	0.01	<b>0.099</b>	<b>0.138</b>	1	1220	1219
<b>T_IYearE2</b>	<b>0.004</b>	0.002	<b>0</b>	<b>0.007</b>	1	1682	1585

**Appendix B-I Table B6: Results from a linear model of unfed beta kittiwakes with a continuous linear and quadratic effect of year fit as a predictor for each growth parameter.** The prefix  $k$  is used for the relative maximum growth rate,  $d$  for the shape of the growth curve (sigmoid when greater than 0),  $T$  for is the age at maximum growth, and  $A$  for the asymptote or maximum size reached during growth. Standard error and 95% highest posterior density intervals are shown. Bolded terms are non-intercept effect terms where 95% confidence intervals did not overlap zero.

Parameter Term	Estimate	Est. Error	l-95%CI	u-95%CI	Rhat	Bulk_ES S	Tail_ES S
d_Intercept	1.764	0.077	1.618	1.913	1.005	978	1269
A_Intercept	4.213	0.029	4.159	4.271	1.003	1048	1194
<b>A_Year</b>	<b>0.017</b>	<b>0.003</b>	<b>0.01</b>	<b>0.024</b>	1.002	1061	1157
<b>A_IYearE2</b>	<b>-0.004</b>	<b>0.001</b>	<b>-0.006</b>	<b>-0.003</b>	1.001	1104	1327
k_Intercept	4.633	0.084	4.467	4.798	1.004	1066	1246
<b>k_Year</b>	<b>-0.071</b>	<b>0.01</b>	<b>-0.091</b>	<b>-0.051</b>	1	1144	1014
k_IYearE2	-0.004	0.002	-0.007	0	1.002	1367	1430
T_Intercept	11.753	0.239	11.289	12.219	1.002	1056	1045
<b>T_Year</b>	<b>0.176</b>	<b>0.018</b>	<b>0.141</b>	<b>0.213</b>	1	1090	1122
<b>T_IYearE2</b>	<b>0.013</b>	<b>0.004</b>	<b>0.005</b>	<b>0.022</b>	1.001	1229	1442

**Appendix B-I Table B7:** Comparison of the leave one out cross-validation information criterion (LOOIC) for competing models for each species and data subset. Delta LOOIC ( $\Delta$ LOOIC) is the LOOIC value of each model subtracted from the highest LOOIC in each species/data subset comparison.  $\Delta$ LOOIC values are displayed with the ascending order. Bolded values indicate models that are the lowest in a comparison or are within 5  $\Delta$ LOOIC of the model with the lowest  $\Delta$ LOOIC. Names of the models indicate the environmental windows included as predictors in that model. "Base" is the baseline model without any predictors, "Ice-cover" is a model with only ice-cover windows as predictors, "Air temp" is the model with only air temperature windows as predictors, and SST is a model with only sea-surface temperature windows as predictors. "All windows" is a model that included all effects from ice-cover and air temperature models (murre) or sea-surface temperature and air temperature models (gulls & kittiwakes) with posterior distributions that did not overlap zero. "NA" for the "All windows" model indicates that none of the effects with posterior distributions overlapped zero in a single environmental variable model (ice-cover, air temperature, sea-surface temperature models). Results for analysis of the murre dataset split at 1999 are in Appendix B-II: Table B2-5.

Overall Model	$\Delta$ LOOIC	PreModel	$\Delta$ LOOIC	PostModel	$\Delta$ LOOIC
<b>Murres</b>		1986-1994		1995-2010; 2017-2018	
All windows	<b>-117.1</b>	Ice cover	<b>-17.4</b>	All windows	<b>-105.9</b>
Ice cover	-77.2	Air Temp	-9.4	Air Temp	-101.3
Air temp	-94.9	Base	-4.3	Ice cover	-100.0
Base	0	All windows	0	Base	0
<b>First-hatched</b>		1998-2007		2008-2018	
<b>Kittiwakes</b>					
<b>Base</b>	<b>-18</b>	Base	<b>-147.9</b>	SST	<b>-7</b>
All windows	-9.6	All windows	<b>-147.3</b>	Air Temp	0
SST	-7.7	Air Temp	<b>-141.8</b>	Base	0
Air Temp	0	SST	0	All windows	NA
<b>Second-hatched</b>		1998-2007		2008-2018	
<b>Kittiwakes</b>					
<b>Air Temp</b>	<b>-67.1</b>	Base	-3.2	<b>SST</b>	<b>-17.6</b>
Base	-0.5	SST	-2	All windows	-8.9
SST	0	Air Temp	0	Air Temp	-5
All windows	NA	All windows	NA	Base	0
<b>Glaucous-winged gulls</b>		2002-2008		2009-2010; 2012; 2016-2018	
SST	<b>-2521.8</b>	SST	<b>-32.4</b>	SST	<b>-2524.4</b>
All windows	<b>-2518.2</b>	Air Temp	0	Air Temp	-2506.6
Air Temp	-2511.5	Base	-12.5	Base	0
Base	0	All windows	NA	All windows	NA

**Appendix B-I Table B8:** Murre LOOIC results with split at 1999. Comparison of the leave one out cross-validation information criterion (LOOIC) for competing models for each species and data subset. Delta LOOIC ( $\Delta$ LOOIC) is the LOOIC value of each model subtract the highest LOOIC in each species/data subset comparison.  $\Delta$ LOOIC values are displayed with the ascending order. Bolded values indicate models that are the lowest in a particular comparison and are within 5  $\Delta$ LOOIC of each other. Names of the models indicate the environmental windows included as predictors in that particular model. “Base” is the baseline model without any predictors, “Ice-cover” is a model with only ice-cover windows as predictors, and “Air temp” is the model with only air temperature windows as predictors. “All windows” is a model that included all effects from ice-cover and air temperature models with posterior distributions that did not overlap zero.

Overall Model	$\Delta$ LOOIC	PreModel	$\Delta$ LOOIC	PostModel	$\Delta$ LOOIC
<b>Murres</b>		1986-1998		1999-2010; 2017-2018	
All windows	<b>-117.1</b>	Air Temp	<b>-105.9</b>	Air Temp	-17.6
Ice cover	-97.2	All windows	-91.3	Base	-14.7
Air temp	-94.9	Ice cover	-87.9	All windows	-11.4
Base	0	Base	0	Ice-cover	0

**Appendix B-I Table B9:** Results of overall murre climwin analysis. Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping, the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

Pre1995	Murre	ICE					
Intercept							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-46.3949	4	2	1.20E-02	1	5	1
Max	-46.5177	4	2	1.50E-02	2	4	1
Min	-48.4564	6	3	1.10E-02	1	5	2
QuadMean	-44.4411	4	2	1.30E-02	1	6	2
QuadMax	-45.4155	4	2	1.70E-02	7	40	19
<b>QuadMin</b>	<b>-49.5396</b>	<b>6</b>	<b>3</b>	<b>1.90E-02</b>	<b>1</b>	<b>67</b>	<b>43</b>
Slope							
<b>Mean</b>	<b>-35.8023</b>	<b>68</b>	<b>66</b>	<b>1.50E-02</b>	<b>5</b>	<b>74</b>	<b>61</b>
Max	-35.763	68	66	2.00E-02	10	68	34
Min	-35.5759	67	66	1.40E-02	6	83	64
QuadMean	-33.9268	66	66	2.00E-02	9	76	61
QuadMax	-34.0184	66	65	3.20E-02	16	69	34
QuadMin	-33.9268	66	66	3.10E-02	8	82	64
Pre1995	Murre	Air temp					
Intercept							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-11.5189	31	30	3.87E-01	80	72	27
Max	-10.0896	66	65	4.40E-01	81	70	34
Min	-11.6644	62	59	2.70E-02	16	65	30
QuadMean	-17.2659	62	60	1.70E-02	4	65	56
QuadMax	-15.97	62	62	9.60E-02	30	69	12
<b>QuadMin</b>	<b>-25.8578</b>	<b>61</b>	<b>1</b>	<b>3.50E-02</b>	<b>7</b>	<b>63</b>	<b>30</b>
Slope							
<b>Mean</b>	<b>-35.8164</b>	<b>32</b>	<b>12</b>	<b>1.30E-02</b>	<b>2</b>	<b>34</b>	<b>11</b>
Max	-23.6005	15	10	1.60E-02	7	29	7
Min	-26.9575	67	0	1.90E-02	10	65	30
QuadMean	-38.1044	32	12	1.50E-02	2	34	12
QuadMax	-26.9525	15	10	5.70E-02	26	56	7
QuadMin	-26.0126	16	15	3.90E-02	11	65	30.5

**Appendix B-I Table B10:** Results of pre1995 murre climwin analysis. Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models summary statistics are reported: **1**) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2**) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3**) the probability of detecting a window just by chance (Pc), and **4**) the extent to which windows have similar explanatory power as the top model (%Confidence). Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models multiple summary statistics are reported. For each grouping the top models are displayed for all growth parameters from our initial growth models (Intercept, Slope).

Overall	Murre	ICE					
Intercept							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-367.698	26	15	1.00E-03	1	26	14
Max	-330.913	23	23	1.00E-03	0	23	23
Min	-362.322	37	23	1.00E-03	2	52	23
QuadMean	<b>-365.732</b>	<b>26</b>	<b>14</b>	<b>1.00E-03</b>	<b>1</b>	<b>26</b>	<b>14</b>
QuadMax	-346.327	23	23	1.00E-03	1	23	23
QuadMin	-366.126	37	23	1.00E-03	2	62	23
Slope							
Mean	-133.811	82	55	1.00E-03	2	62	23
Max	-142.383	66	13	1.00E-03	4	63	13
Min	-139.262	81	60	1.00E-03	2	75	60
QuadMean	-136.013	81	56	1.00E-03	4	75	56
QuadMax	-142.674	66	14	1.00E-03	4	64	13
QuadMin	<b>-142.535</b>	<b>81</b>	<b>60</b>	<b>1.00E-03</b>	<b>2</b>	<b>76</b>	<b>60</b>
Overall	Murre	Air Temp					
Intercept							
Model	deltaAIC	BestOpen	BestClose	Pc	%Confidence	95% Open	95% Close
Mean	-91.8544	38	9	1.00E-03	3	36	13
Max	-65.8417	26	24	1.00E-03	1	26	9
Min	-52.1854	37	30	1.00E-03	1	36	29
QuadMean	-99.7156	98	87	1.00E-03	1	97	87
QuadMax	-116.893	100	85	1.00E-03	1	100	85.5
QuadMin	<b>-139.914</b>	<b>63</b>	<b>1</b>	<b>1.00E-03</b>	<b>1</b>	<b>63</b>	<b>8.5</b>
Slope							
Mean	-54.3967	31	8	1.00E-03	2	31	8
Max	<b>-72.9148</b>	<b>26</b>	<b>9</b>	<b>1.00E-03</b>	<b>1</b>	<b>27.5</b>	<b>7.5</b>
Min	-32.3011	12	12	1.00E-03	1	10	10
QuadMean	-59.1547	17	9	1.00E-03	1	17	9
QuadMax	-79.4149	14	10	1.00E-03	1	15	9
QuadMin	-62.0626	17	0	1.00E-03	1	17	0

**Appendix B-I Table B11:** Results of post1995 murre climwin analysis. Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models summary statistics are reported: **1**) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2**) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3**) the probability of detecting a window just by chance (Pc), and **4**) the extent to which windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Intercept, Slope).

Post1995	Murre	ICE						
Intercept								
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Mean	-364.198	62	11	2.00E-03	3	62	7	
Max	-297.729	50	41	2.00E-03	1	50	41	
Min	-307.677	37	23	3.00E-03	2	60	23	
<b>QuadMean</b>	<b>-379.703</b>	<b>58</b>	<b>0</b>	<b>6.00E-03</b>	<b>3</b>	<b>58</b>	<b>6</b>	
QuadMax	-355.214	34	4	4.00E-03	1	34	2.5	
QuadMin	-311.752	25	23	1.60E-02	8	63.5	44	
Slope								
Mean	-117.396	60	60	3.00E-03	5	69	53	
Max	<b>-126.346</b>	<b>60</b>	<b>14</b>	<b>2.00E-03</b>	<b>2</b>	<b>60</b>	<b>13</b>	
Min	-121.87	77	59	3.00E-03	2	72	58	
QuadMean	-117.472	60	60	3.00E-03	5	73	54	
QuadMax	-125.448	60	14	7.00E-03	2	60	14	
QuadMin	-123.671	77	59	2.00E-03	2	74	59	
Post1995	Murre	Air Temp						
Intercept								
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Mean	-136.622	100	95	2.00E-03	1	100	95	
Max	-151.544	100	97	3.00E-03	0	100	97	
Min	-104.496	100	100	2.00E-03	1	100	98	
<b>QuadMean</b>	<b>-266.004</b>	<b>98</b>	<b>89</b>	<b>6.00E-03</b>	<b>1</b>	<b>98</b>	<b>89</b>	
QuadMax	-174.692	98	93	7.00E-03	1	99	93	
QuadMin	-231.349	94	88	6.00E-03	2	94	47	
Slope								
Mean	-67.0924	61	51	4.00E-03	2	59	49.5	
Max	-75.6905	12	8	5.00E-03	4	79	52	
Min	-67.6523	52	1	3.00E-03	1	53	7	
QuadMean	-71.4749	17	9	7.00E-03	2	55.5	49	
QuadMax	<b>-82.3457</b>	<b>14</b>	<b>9</b>	<b>4.00E-03</b>	<b>4</b>	<b>77</b>	<b>52</b>	
QuadMin	-75.7862	17	0	3.00E-03	1	53	1	

**Appendix B-I Table B12:** Results of pre1999 murre climwin analysis. Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models multiple summary statistics are reported: 1) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), 2) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, 3) the probability of detecting a window just by chance (Pc), and 4) the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Intercept, Slope).

Pre1999	Murre	ICE					
Intercept							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-56.9809	4	1	6.00E-03	1	3.5	1
Max	-56.0699	2	1	7.00E-03	1	2	1
Min	-57.6004	3	2	6.00E-03	1	5	2
QuadMean	-59.6384	2	1	7.00E-03	1	3	1
<b>QuadMax</b>	<b>-62.8794</b>	<b>2</b>	<b>1</b>	<b>9.00E-03</b>	<b>1</b>	<b>2</b>	<b>1</b>
QuadMin	-56.4682	3	2	8.00E-03	1	5	2
Slope							
Mean	-73.0208	66	66	1.00E-02	11	76	54
Max	-73.0208	66	66	1.70E-02	13	66	29
Min	-73.3553	83	61	9.00E-03	6	81	62
QuadMean	-80.8566	66	66	8.00E-03	5	72	58
<b>QuadMax</b>	<b>-80.8566</b>	<b>66</b>	<b>66</b>	<b>1.20E-02</b>	<b>8</b>	<b>67</b>	<b>34</b>
QuadMin	-80.8566	66	66	1.30E-02	5	84	62
Pre1999	Murre	Air temp					
Intercept							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-23.5727	6	3	1.10E-02	3	26	13
Max	-26.5188	6	3	9.00E-03	6	30	10
Min	-20.9598	4	4	1.40E-02	13	89	31
QuadMean	-40.1615	22	12	1.00E-02	1	23	11
QuadMax	-45.0314	12	9	1.70E-02	5	66	1
QuadMin	-64.2125	61	1	9.00E-03	1	62	7
Slope							
Mean	-20.5684	32	15	7.00E-03	4	30	15
Max	-21.6704	26	8	1.20E-02	11	34	8
Min	-17.4711	71	71	1.50E-02	15	73	36
QuadMean	-30.8769	97	96	1.10E-02	1	99	89
QuadMax	-27.4263	96	96	4.90E-02	17	63	6
QuadMin	-51.9289	100	94	3.60E-02	4	100	48

**Supporting Information Table S1-13:** Results of post1999 murre climwin analysis. Environmental variable analyzed is divided into horizontal sections (Ice-cover, air temp). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Intercept, Slope).

Post1999	Murre	ICE						
Intercept								
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Mean	-192.748	62	0	1.00E-02	3	61	7	
Max	-169.911	23	23	5.00E-03	1	23	23	
Min	-207.059	37	23	7.00E-03	2	62	23	
QuadMean	-212.08	24	24	9.00E-03	2	59.5	4	
QuadMax	<b>-213.86</b>	<b>24</b>	<b>22</b>	<b>8.00E-03</b>	<b>1</b>	<b>24</b>	<b>20.5</b>	
QuadMin	-212.08	24	24	1.40E-02	2	53	23	
Slope								
Mean	-64.5816	83	57	7.00E-03	6	81	59	
Max	-81.3826	79	47	8.00E-03	5	79	26	
Min	-63.3379	77	60	5.00E-03	3	75	60	
QuadMean	-62.5852	83	57	1.10E-02	7	81	59	
QuadMax	<b>-85.8399</b>	<b>79</b>	<b>37</b>	<b>1.00E-02</b>	<b>5</b>	<b>79</b>	<b>23</b>	
QuadMin	-61.641	77	60	8.00E-03	4	73	60	
Post1999	Murre	Air Temp						
Intercept								
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Mean	-77.644	100	95	5.00E-03	1	40	24	
Max	-89.4554	100	97	5.00E-03	1	100	97	
Min	-65.2581	40	30	6.00E-03	1	40	31	
QuadMean	-190.687	98	89	1.10E-02	1	98.5	89	
QuadMax	-130.64	100	90	7.00E-03	1	99	90	
QuadMin	-159.47	94	90	1.10E-02	1	94	89.5	
Slope								
Mean	-83.6326	13	6	6.00E-03	1	13	5.5	
Max	-78.2976	11	8	6.00E-03	1	12	7	
Min	-70.8428	9	9	7.00E-03	1	9.5	9	
QuadMean	-83.3586	13	6	6.00E-03	1	13	5	
QuadMax	-77.1842	11	8	1.50E-02	1	12	7	
QuadMin	-70.1603	9	9	1.00E-02	1	9.5	9	

**Appendix B-I Table B14:** Results of overall climwin analysis for gulls. The table is divided into horizontal sections by environmental variable (SST, air temp). For these best models summary statistics are reported: **1**) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2**) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before a nestling was 50 days old, **3**) the probability of detecting a window by chance (Pc), and **4**) the extent to which several windows have similar explanatory power (%Confidence). Top models for parameters from initial growth models are shown (Asymptote, Inflection Point, Growth Rate).

Overall Dataset	GWGU	SST					
Asymptote Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-19.64	48	43	3.10E-02	27	83	40
Max	-26.67	56	41	1.20E-02	7	98	41
Min	-21.42	68	8	1.20E-02	9	68	34
QuadMean	-20.57	48	40	1.70E-02	13	68	40
<b>QuadMax</b>	<b>-28.54</b>	<b>56</b>	<b>41</b>	<b>1.10E-02</b>	<b>6</b>	<b>99</b>	<b>40</b>
QuadMin	-22.32	65	50	2.00E-02	8	66	35
Inflection Point							
Mean	-16.87	15	150	6.10E-02	39	94	41
Max	-19.77	58	41	1.40E-02	8	100	42
Min	-21.34	150	143	1.40E-02	12	140	50
QuadMean	-39.36	38	35	1.00E-02	2	44	33
QuadMax	-47.42	50	36	1.70E-02	7	98	38
<b>QuadMin</b>	<b>-45.24</b>	<b>25</b>	<b>0</b>	<b>1.30E-02</b>	<b>1</b>	<b>26.5</b>	<b>4.5</b>
Growth Rate							
Mean	-37.58	83	83	8.00E-03	1	86	79
Max	-44.3	85	82	1.10E-02	4	117	79
Min	-37.58	84	81	8.00E-03	1	84	81
QuadMean	-106.44	144	126	1.30E-02	2	145	124
<b>QuadMax</b>	<b>-110.96</b>	<b>144</b>	<b>134</b>	<b>9.00E-03</b>	<b>1</b>	<b>146</b>	<b>134</b>
QuadMin	-96.21	139	121	1.10E-02	5	138	88
Overall Dataset	GWGU	Air Temp					
Asymptote Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-25.75	49	46	1.00E-02	5	58	39
<b>Max</b>	<b>-35.4</b>	<b>52</b>	<b>46</b>	<b>1.10E-02</b>	<b>1</b>	<b>52</b>	<b>45</b>
Min	-24	49	49	2.00E-02	18	70	33
QuadMean	-26.17	49	46	1.10E-02	4	56	40
QuadMax	-35.95	52	46	1.90E-02	1	52	44
QuadMin	-43	49	49	1.40E-02	10	65	25
Inflection Point							
Mean	-26.82	45	45	9.00E-03	5	106	94
Max	-39.24	126	100	8.00E-03	2	131	99
Min	-26.82	45	45	9.00E-03	3	48	36
QuadMean	-45.34	40	35	1.20E-02	1	43	35
<b>QuadMax</b>	<b>-72.7</b>	<b>103</b>	<b>97</b>	<b>1.00E-02</b>	<b>1</b>	<b>105.5</b>	<b>97</b>
QuadMin	-47.95	19	11	2.00E-02	1	19	7
Growth Rate							
Mean	-31.68	83	79	9.00E-03	4	113	80
Max	-27.13	81	81	1.00E-02	5	130	103

Min	-43.9	109	107	1.00E-02	0	109	107
QuadMean	-50.15	150	135	1.30E-02	1	149	124
<b>QuadMax</b>	<b>-86.87</b>	<b>150</b>	<b>140</b>	<b>8.00E-03</b>	<b>1</b>	<b>150</b>	<b>140</b>
QuadMin	-42.76	109	107	1.20E-02	2	113	77

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**Appendix B-I Table B15:** Results of pre 2009 climwin analysis for gulls. The table is divided into horizontal sections by environmental variable (SST, air temp). For these best models summary statistics are reported: 1) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), 2) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before a nestling was 50 days old, 3) the probability of detecting a window by chance (Pc), and 4) the extent to which several windows have similar explanatory power (%Confidence). Top models for parameters from initial growth models are shown (Asymptote, Inflection Point, Growth Rate).

Pre2009	GWGU	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-15.42	64	64	0.173	58	122	60
Max	-15.42	64	64	0.11	40	116	63
Min	-19.51	141	112	0.067	32	136	52
QuadMean	-17.73	139	135	0.237	6	62	120
QuadMax	-20.51	10	2	0.02	5	87	64
QuadMin	-18.08	7	6	0.026	8	48	19
Timing of Maximum Growth							
Mean	-29.82	45	38	0.019	8	54	32
Max	-38.22	61	39	0.018	11	98	37
Min	-27.93	42	42	0.018	8	67	32
QuadMean	-36.05	30	5	0.022	11	47	17
QuadMax	-42.31	61	39	0.043	23	100	30
QuadMin	-32.31	40	38	0.021	6	67	32
Maximum Growth Rate							
Mean	-34.54	143	138	0.012	2	146	135
Max	-33.65	139	139	0.013	1	145	140
Min	-38.98	142	138	0.028	13	144	73
QuadMean	-48.64	145	139	0.013	2	146	139
QuadMax	-49.06	145	143	0.017	1	145	140
QuadMin	-52	29	6	0.022	13	145	68
Pre2009	GWGU	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-14.87	127	127	1.92E-01	61	121	57
Max	-14.87	127	127	5.50E-02	32	116	90
Min	-15.11	67	63	6.30E-02	36	104	43
QuadMean	-19.18	87	76	1.65E-01	50	119	59
QuadMax	-17.46	150	142	8.90E-02	35	119	70
QuadMin	-16.5	85	75	1.55E-01	98	50	43
Timing of Maximum Growth							
Mean	-71.65	150	97	1.50E-02	8	132	100
Max	-94.23	150	140	1.20E-02	1	135	99
Min	-67.04	119	117	2.50E-02	16	120	52
QuadMean	-93.64	149	100	1.80E-02	4	144	102
QuadMax	-110.34	120	98	1.60E-02	1	131	98
QuadMin	-86.12	105	103	1.60E-02	3	117	49
Maximum Growth Rate							
Mean	-77.28	148	119	1.10E-02	2	148	120
Max	-95.33	148	137	1.10E-02	1	148	135

Min	-76.23	120	113	1.40E-02	6	119	59
QuadMean	-77.53	148	119	1.10E-02	2	148	121
QuadMax	-100.89	148	137	2.00E-02	1	148	134
QuadMin	-75.35	133	129	2.30E-02	9	121	62

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**Appendix B-I Table B16:** Results of post 2009 climwin analysis for gulls. The table is divided into horizontal sections by environmental variable (SST, air temp). For these best models summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before a nestling was 50 days old, **3)** the probability of detecting a window by chance (Pc), and **4)** the extent to which several windows have similar explanatory power (%Confidence). Top models for parameters from initial growth models are shown (Asymptote, Inflection Point, Growth Rate).

Post2009	GWGU	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-6.48	47	47	5.06E-01	90	102	39
Max	-7.34	48	43	4.07E-01	82	100	35
Min	-6.88	47	46	4.90E-01	89	101	42
<b>QuadMean</b>	<b>-17.83</b>	<b>6</b>	<b>6</b>	<b>2.20E-02</b>	<b>6</b>	<b>26</b>	<b>8</b>
QuadMax	-15.01	27	2	1.51E-01	50	89	24
QuadMin	-13.74	15	10	2.04E-01	58	86	38
Timing of Maximum Growth							
Mean	-17.72	42	39	2.30E-02	15	57	24
Max	-23.08	61	39	1.90E-02	12	99	37
Min	-17.21	41	41	3.50E-02	24	60	28
QuadMean	-21.61	42	39	4.60E-02	24	64	37
<b>QuadMax</b>	<b>-34.93</b>	<b>46</b>	<b>97</b>	<b>2.90E-02</b>	<b>26</b>	<b>97</b>	<b>29</b>
QuadMin	-21.37	40	39	7.50E-02	36	130	61
Maximum Growth Rate							
Mean	-48.25	143	138	1.40E-02	2	145	134
Max	-47.3	138	138	1.10E-02	1	144	139
Min	-52.72	141	138	2.50E-02	12	144	71
QuadMean	<b>-64.05</b>	<b>141</b>	<b>139</b>	<b>1.30E-02</b>	<b>2</b>	<b>144</b>	<b>136</b>
QuadMax	-64.08	140	139	2.20E-02	2	141	125
QuadMin	-64.08	140	139	2.00E-02	12	144	70
Post2009	GWGU	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-8.72	50	46	6.05E-01	90	105	38
Max	-8.72	50	46	4.22E-01	83	103	36
Min	-8.2	7	7	4.76E-01	86	100	41
QuadMean	-12.39	21	1	1.69E-01	52	77	22.5
QuadMax	-16.36	25	5	8.30E-02	21	110	59
QuadMin	-8.1	8	6	4.07E-01	73	95	40
Inflection Point							
Mean	-38.93	42	41	1.40E-02	4	50	32
Max	-41.79	60	37	1.80E-02	9	95	36
Min	<b>-41.42</b>	<b>43</b>	<b>41</b>	<b>1.20E-02</b>	<b>1</b>	<b>43</b>	<b>40</b>
QuadMean	-44.02	42	41	2.00E-02	7	50	21
QuadMax	-44.89	55	41	2.10E-02	12	101	36
QuadMin	-43.23	41	41	1.50E-02	2	42	24
Maximum Growth Rate							
Mean	-27.85	144	144	1.30E-02	4	144	127
Max	-27.85	144	144	1.40E-02	3	139	128
Min	-35.37	149	143	1.20E-02	1	146	139
QuadMean	-43.38	147	138	1.50E-02	2	147	132
<b>QuadMax</b>	<b>-52</b>	<b>112</b>	<b>96</b>	<b>1.80E-02</b>	<b>3</b>	<b>129</b>	<b>95</b>
QuadMin	-45.39	21	12	2.10E-02	8	120	57.5

**Appendix B-I Table B17:** Results of overall climwin analysis for first-hatched kittiwakes. The table is divided into horizontal sections by environmental variable (SST, air temp). For these best models summary statistics are reported: **1**) the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2**) the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before a nestling was 40 days old, **3**) the probability of detecting a window by chance (Pc), and **4**) the extent to which several windows have similar explanatory power (%Confidence). Top models for parameters from initial growth models are shown (Asymptote, Inflection Point, Growth Rate).

Overall Dataset	Alpha	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-118.8	120	0	2.0E-03	8	104	4
Max	-122.0	119	10	1.5E-03	11	80.5	12
Min	-118.5	120	119	1.6E-03	1	119	112
QuadMean	-119.5	120	0	4.7E-03	11	108	9
QuadMax	-121.8	96	91	4.7E-03	11	78	12
QuadMin	<b>-120.7</b>	<b>14</b>	<b>2</b>	<b>1.9E-03</b>	<b>4</b>	<b>91</b>	<b>37</b>
Inflection Point							
Mean	-205.4	95	89	1.1E-03	2	96	83
Max	-237.3	119	91	1.3E-03	1	109	91
Min	-196.9	93	93	1.2E-03	1	93	92
QuadMean	-224.6	95	89	1.8E-03	1	95	88
QuadMax	<b>-264.0</b>	<b>119</b>	<b>90</b>	<b>1.3E-03</b>	<b>1</b>	<b>112</b>	<b>90</b>
QuadMin	-212.8	93	93	1.3E-03	1	93	93
Growth Rate							
Mean	-281.9	95	90	1.7E-03	1	95	89
Max	-331.2	107	91	1.0E-03	1	110.5	91
Min	-273.9	93	93	1.8E-03	0	93	93
QuadMean	-308.5	95	89	1.8E-03	1	95	89
QuadMax	<b>-375.6</b>	<b>119</b>	<b>91</b>	<b>9.9E-04</b>	<b>1</b>	<b>112</b>	<b>91</b>
QuadMin	-294.9	93	93	8.7E-04	0	93	93
Overall Dataset	Alpha	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-126.3	61	47	2.0E-03	6	63	22
Max	<b>-147.2</b>	<b>114</b>	<b>11</b>	<b>2.7E-03</b>	<b>12</b>	<b>91</b>	<b>12</b>
Min	-117.2	53	51	1.1E-03	2	54	38
QuadMean	-124.8	61	47	7.6E-03	10	99	16
QuadMax	-146.5	114	11	3.6E-03	11	94	11
QuadMin	-115.2	53	51	3.3E-03	4	55	25
Inflection Point							
Mean	-284.7	120	63	1.4E-03	1	118	62
Max	-259.7	106	91	1.4E-03	1	107	91
Min	-232.7	120	64	1.3E-03	2	120	42
QuadMean	-290.9	120	64	1.5E-03	1	119	62
QuadMax	-262.4	106	91	1.7E-03	1	107	91
QuadMin	<b>-309.6</b>	<b>97</b>	<b>68</b>	<b>5.1E-03</b>	<b>3</b>	<b>97</b>	<b>39</b>
Growth Rate							
Mean	-444.0	116	63	1.2E-03	2	112	63
Max	-372.5	40	25	1.1E-03	1	40	25
Min	-389.0	106	65	1.9E-03	8	107	40
QuadMean	-462.2	120	64	1.6E-03	1	118	64
QuadMax	-370.5	40	25	1.6E-03	1	40	25
QuadMin	<b>-556.2</b>	<b>97</b>	<b>68</b>	<b>2.0E-03</b>	<b>3</b>	<b>97</b>	<b>35</b>

**Appendix B-I Table B18:** Results of pre2008 climwin analysis for first-hatched kittiwakes. For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Asymptote, Inflection Point, Growth Rate).

Pre2008	Alpha	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-13.52	46	46	3.39E-01	76	86	27
Max	-16.5	60	45	7.80E-02	38	78	13
Min	-13.52	46	46	1.22E-01	50	63	27
QuadMean	-16.78	92	91	3.90E-01	66	95	33
QuadMax	-17.11	94	91	4.80E-02	29	88	11
<b>QuadMin</b>	<b>-16.81</b>	<b>92</b>	<b>87</b>	<b>2.60E-02</b>	<b>11</b>	<b>91</b>	<b>42</b>
Timing of Maximum Growth							
Mean	-216.56	29	25	1.40E-02	1	30.5	23
<b>Max</b>	<b>-229.26</b>	<b>47</b>	<b>8</b>	<b>1.80E-02</b>	<b>7</b>	<b>74</b>	<b>9</b>
Min	-214.66	27	27	1.10E-02	1	28	26.5
QuadMean	-224.41	29	25	1.40E-02	1	29	25
QuadMax	-230.49	47	8	1.80E-02	7	74	9
QuadMin	-226.26	29	26	1.70E-02	1	29	26
Maximum Growth Rate							
Mean	-265.12	29	26	1.30E-02	1	29	26
Max	-290.49	34	24	1.20E-02	3	79.5	8
Min	-263.72	27	27	1.30E-02	1	27	27
QuadMean	-264.16	29	26	1.20E-02	1	29	26
<b>QuadMax</b>	<b>-294.62</b>	<b>47</b>	<b>8</b>	<b>1.70E-02</b>	<b>3</b>	<b>73</b>	<b>8</b>
QuadMin	-262.05	27	27	1.50E-02	1	27	27
Pre2008	Alpha	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-9.91	33	33	3.41E-01	75	80	25
<b>Max</b>	<b>-15.04</b>	<b>64</b>	<b>28</b>	<b>8.70E-02</b>	<b>40</b>	<b>86</b>	<b>19</b>
Min	-10.07	115	113	4.00E-01	80	90	32
QuadMean	-15.08	4	1	8.00E-02	27	51	19
QuadMax	-18.36	51	19	0.13	43	81	19
QuadMin	-15.53	4	2	1.00E-01	42	93	28
Timing of Maximum Growth							
Mean	-190.9	29	24	1.10E-02	1	29	23
<b>Max</b>	<b>-227.78</b>	<b>38</b>	<b>24</b>	<b>1.30E-02</b>	<b>1</b>	<b>37</b>	<b>24</b>
Min	-160.06	28	25	1.70E-02	3	104	25
QuadMean	-192.22	29	23	1.00E-02	1	30	22
QuadMax	-228.54	37	24	4.00E-02	2	40	26
QuadMin	-219.45	104	68	1.00E-02	5	104	39
Maximum Growth Rate							
Mean	-248.42	120	65	1.20E-02	1	119	64
Max	-258.03	38	24	1.10E-02	1	37	25
Min	-199.91	105	64	1.50E-02	5	104	34.5
QuadMean	-245.52	120	65	1.00E+00	2	119	64
QuadMax	-274.6	79	27	2.00E-02	3	97	26
<b>QuadMin</b>	<b>-348.78</b>	<b>117</b>	<b>68</b>	<b>2.00E-02</b>	<b>4</b>	<b>119</b>	<b>40</b>

**Appendix B-I Table B19:** Results of post2008 climwin analysis for first-hatched kittiwakes.

Environmental variable analyzed is divided into horizontal sections (SST, air temp). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Asymptote, Inflection Point, Growth Rate).

Post2008	Alpha Unfed	SST					
Asymptote Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-157.03	120	0	1.10E-02	5	107	4
Max	-131.39	59	52	2.50E-02	19	84	13
Min	-128.77	50	48	2.40E-02	17	82	33
<b>QuadMean</b>	<b>-164.98</b>	<b>120</b>	<b>0</b>	<b>1.00E-02</b>	<b>6</b>	<b>115</b>	<b>13</b>
QuadMax	-132.81	59	52	3.00E-02	17	87	16
QuadMin	-137.67	83	43	2.00E-02	15	82	39
Timing of Maximum Growth							
Mean	-148.42	91	83	9.00E-03	2	94	82
Max	-154.17	119	84	1.00E-02	3	107	85
Min	-141.27	85	85	1.40E-02	6	88	49
QuadMean	-182.27	95	83	1.00E-02	2	95	83
<b>QuadMax</b>	<b>-192</b>	<b>119</b>	<b>86</b>	<b>1.00E-02</b>	<b>2</b>	<b>111</b>	<b>86</b>
QuadMin	-172.91	88	76	2.00E-02	3	87	56
Maximum Growth Rate							
Mean	-278.96	92	79	9.00E-03	2	93	80
Max	-283.18	93	85	1.10E-02	1	102.5	85
Min	-277.67	86	67	1.10E-02	3	86	42
<b>QuadMean</b>	<b>-358.42</b>	<b>91</b>	<b>83</b>	<b>1.10E-02</b>	<b>1</b>	<b>93</b>	<b>81</b>
QuadMax	-373.4	100	86	1.10E-02	1	106.5	86
QuadMin	-359.43	86	67	1.20E-02	2	86	58
Post2008	Alpha Unfed	Air Temp					
Asymptote Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-167.83	60	49	3.60E-02	28	82	24
Max	-153.35	114	6	1.70E-02	13	87	8
Min	-161.81	58	48	1.10E-02	2	59	40
<b>QuadMean</b>	<b>-165.96</b>	<b>61</b>	<b>1</b>	<b>3.70E-02</b>	<b>25</b>	<b>75</b>	<b>16</b>
QuadMax	-157.092	114	6	3.10E-02	9	99	7
QuadMin	-160.17	58	48	2.60E-02	6	58	24
Inflection Point							
Mean	-158.61	120	81	1.10E-02	4	112	83
Max	-149.35	116	94	1.00E-02	3	113	91
Min	-129.57	95	91	1.00E-02	1	95	88.5
QuadMean	-162.7	120	81	1.40E-02	3	112	82
<b>QuadMax</b>	<b>-171.04</b>	<b>118</b>	<b>96</b>	<b>1.00E-02</b>	<b>1</b>	<b>115</b>	<b>96</b>
QuadMin	-132.08	95	91	1.20E-02	2	95	72.5
Maximum Growth Rate							
Mean	-318.38	99	85	1.00E-02	2	101	83
Max	-243.78	88	82	1.00E-02	2	106.5	81
Min	-280.5	95	85	1.00E-02	1	95	83

QuadMean	-342.89	102	81	1.50E-02	1	102	81
QuadMax	-277.9	103	80	1.10E-02	1	109	80
<b>QuadMin</b>	<b>-348.78</b>	<b>117</b>	<b>68</b>	<b>2.50E-02</b>	<b>4</b>	<b>119</b>	<b>40</b>

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**Appendix B-I Table B20:** Results of overall climwin analysis for second-hatched kittiwakes.

Environmental variable analyzed is divided into horizontal sections (SST, air temp). For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Asymptote, Inflection Point, Growth Rate).

Overall Dataset	Beta	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-287.1	120	0	2.0E-03	4	82.5	1
Max	-281.8	60	27	1.5E-03	4	80	27
Min	-274.1	31	0	1.0E-03	9	30	2
QuadMean	<b>-317.9</b>	<b>120</b>	<b>0</b>	<b>1.9E-03</b>	<b>3</b>	<b>115</b>	<b>4</b>
QuadMax	-286.0	60	27	7.3E-03	9	81	25
QuadMin	-272.8	31	0	2.2E-03	9	30	3
Inflection Point							
Mean	-139.7	94	94	1.1E-03	1	95	91
Max	<b>-155.6</b>	<b>114</b>	<b>92</b>	<b>1.2E-03</b>	<b>1</b>	<b>113</b>	<b>91</b>
Min	-139.7	94	94	1.2E-03	1	94	94
QuadMean	-137.9	94	94	1.4E-03	1	95	91
QuadMax	-153.6	114	92	1.3E-03	1	112.5	91
QuadMin	-137.9	94	94	3.0E-03	1	94	94
Growth Rate							
Mean	-168.3	94	94	1.3E-03	1	95	92
Max	<b>-183.7</b>	<b>116</b>	<b>93</b>	<b>1.2E-03</b>	<b>1</b>	<b>112.5</b>	<b>92</b>
Min	-168.3	94	94	9.9E-04	1	94	94
QuadMean	-166.4	94	94	1.6E-03	1	95	92
QuadMax	-182.8	116	93	2.0E-03	1	113	92
QuadMin	-166.4	94	94	1.6E-03	1	94	94
Overall Dataset	Beta	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-317.2	63	6	1.0E-03	2	63	6
Max	-318.1	101	51	1.5E-03	4	107	52
Min	-295.2	55	40	1.1E-03	1	56	38
QuadMean	<b>-332.3</b>	<b>62</b>	<b>6</b>	<b>1.7E-03</b>	<b>1</b>	<b>62</b>	<b>6</b>
QuadMax	-324.5	100	0	6.9E-03	8	104	45
QuadMin	-293.4	55	40	2.7E-03	1	55	37
Inflection Point							
Mean	-197.7	120	62	1.3E-03	3	118	61
Max	-193.0	119	102	1.1E-03	1	119	107
Min	-189.3	106	94	2.9E-03	12	111	29.5
QuadMean	-197.2	120	116	2.4E-03	3	118	65
QuadMax	-196.0	119	117	1.3E-03	1	118	101
QuadMin	<b>-261.2</b>	<b>107</b>	<b>0</b>	<b>3.3E-03</b>	<b>1</b>	<b>107.5</b>	<b>0</b>
Growth Rate							
Mean	-272.7	102	93	1.2E-03	1	102	93
Max	-215.2	110	88	1.2E-03	2	110.5	88
Min	-321.3	104	93	1.2E-03	1	104.5	93.5

QuadMean	-271.3	102	93	1.8E-03	1	103	93
QuadMax	-213.7	110	88	2.3E-03	2	110.5	88
QuadMin	<b>-390.2</b>	<b>99</b>	<b>70</b>	<b>4.5E-03</b>	<b>5</b>	<b>101</b>	<b>39</b>

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**Appendix B-I Table B21:** Results of pre2008 climwin analysis for second-hatched kittiwakes. For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters from our initial growth models (Asymptote, Inflection Point, Growth Rate).

Pre2009	Beta	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-30.74	30	30	7.60E-02	35	66	11
Max	-30.78	15	8	5.00E-02	31	72	14
Min	-30.74	30	30	1.90E-02	11	33	14
QuadMean	-43.86	15	7	3.60E-02	24	78	8
QuadMax	<b>-43.64</b>	<b>16</b>	<b>8</b>	<b>3.40E-02</b>	<b>9</b>	<b>72</b>	<b>9</b>
QuadMin	-33.72	31	30	2.70E-02	13	84.5	22
Timing of Maximum Growth							
Mean	-165.36	29	29	1.50E-02	3	34	17
Max	-187.38	34	25	1.20E-02	2	37	19
Min	-174.55	25	12	1.20E-02	1	26	13
QuadMean	-169.91	29	29	3.50E-02	6	76	10
QuadMax	<b>-188.38</b>	<b>34</b>	<b>25</b>	<b>1.80E-02</b>	<b>1</b>	<b>35</b>	<b>23</b>
QuadMin	-177.47	28	13	1.50E-02	1	28	13
Maximum Growth Rate							
Mean	-210.2	29	28	1.00E-02	1	30	28
Max	<b>-230.8</b>	<b>32</b>	<b>25</b>	<b>1.20E-02</b>	<b>1</b>	<b>33</b>	<b>22</b>
Min	-209.43	29	29	1.40E-02	1	28	20.5
QuadMean	-208.66	29	28	1.30E-02	1	30	27
QuadMax	-231.49	32	25	1.30E-02	1	33	22
QuadMin	-207.4	29	29	1.40E-02	1	28	20.5
Pre2009	Beta	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-26.93	30	25	5.10E-02	31	100	20
Max	-31.49	104	85	3.50E-02	22	91	26
Min	-28.2	32	25	1.50E-02	6	34	20
QuadMean	<b>-43.29</b>	<b>33</b>	<b>28</b>	<b>1.40E-02</b>	<b>2</b>	<b>33</b>	<b>24</b>
QuadMax	-41.91	33	30	1.80E-02	6	53	27
QuadMin	-37.05	31	29	1.80E-02	2	32	20
Timing of Maximum Growth							
Mean	-160.65	106	94	1.20E-02	1	106	94
Max	-155.88	40	26	1.30E-02	1	36.5	25.5
Min	-141.16	106	93	1.60E-02	1	105	94
QuadMean	-176.76	100	69	1.40E-02	2	101	68
QuadMax	-154.73	40	23	1.40E-02	1	38	25
QuadMin	<b>-218.05</b>	<b>100</b>	<b>75</b>	<b>2.30E-02</b>	<b>7</b>	<b>102</b>	<b>39</b>
Maximum Growth Rate							
Mean	-179.69	106	93	1.10E-02	1	106	93.5
Max	-151.99	106	76	1.40E-02	2	108	76
Min	-177.85	104	93	1.40E-02	1	105	93

QuadMean	-177.77	106	93	1.50E-02	2	100	70
QuadMax	-152.49	106	76	1.80E-02	2	111	76
<b>QuadMin</b>	<b>-251.35</b>	<b>100</b>	<b>84</b>	<b>1.60E-02</b>	<b>3</b>	<b>100</b>	<b>42</b>

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**Appendix B-I Table B22:** Results of post2008 climwin analysis for second-hatched kittiwakes. For each of these best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 40 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all parameters (Asymptote, Inflection Point, Growth Rate).

Post2009	Beta	SST					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-248	120	0	1.10E-02	4	108.5	5
Max	-229.23	60	30	1.30E-02	6	79	29
Min	-230.98	37	0	1.00E-02	4	52	17
<b>QuadMean</b>	<b>-270.89</b>	<b>120</b>	<b>0</b>	<b>1.30E-02</b>	<b>3</b>	<b>116</b>	<b>8</b>
QuadMax	-227.52	60	30	2.20E-02	6	82	29
QuadMin	-231.99	37	14	1.20E-02	4	52	14
Timing of Maximum Growth							
Mean	-69.05	94	87	1.00E-02	2	94	85
Max	-85.16	107	87	1.00E-02	2	107	86
Min	-68.58	91	91	1.60E-02	6	91	52
QuadMean	-88.7	94	85	1.10E-02	2	94	85
QuadMax	<b>-103.59</b>	<b>107</b>	<b>87</b>	1.50E-02	<b>2</b>	<b>110</b>	<b>86</b>
QuadMin	-81.6	87	87	2.00E-02	8	89	48
Maximum Growth Rate							
Mean	-132.22	94	85	1.10E-02	3	94	82
Max	-147.21	96	87	1.00E-02	2	103	86
Min	-124.47	91	91	1.40E-02	9	88	44
QuadMean	-163.09	95	85	1.00E-02	2	94.5	84
<b>QuadMax</b>	<b>-178.92</b>	<b>101</b>	<b>87</b>	<b>1.10E-02</b>	<b>1</b>	<b>103</b>	<b>86</b>
QuadMin	-152.94	88	71	1.80E-02	4	87	38.5
Post2009	Beta	Air Temp					
Asymptote							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close
Mean	-284.72	63	50	1.40E-02	5	66	37
Max	-255.69	80	31	1.00E-02	2	93	31
Min	-298.13	54	37	1.00E-02	2	54	20.5
QuadMean	-287.14	64	50	1.60E-02	5	67	34
QuadMax	-261.13	24	0	1.30E-02	4	91	29
<b>QuadMin</b>	<b>-306.14</b>	<b>56</b>	<b>42</b>	<b>1.30E-02</b>	<b>2</b>	<b>54</b>	<b>24</b>
Inflection Point							
Mean	-94.71	102	93	1.10E-02	4	110	90
<b>Max</b>	<b>-158.44</b>	<b>112</b>	<b>87</b>	<b>9.00E-03</b>	<b>1</b>	<b>114</b>	<b>86</b>
Min	-72.19	105	102	9.00E-03	1	103	100
QuadMean	-97.27	120	86	1.30E-02	4	110	88
QuadMax	-156.4	112	87	1.30E-02	1	114	86
QuadMin	-73.78	106	103	1.40E-02	1	106	103
Maximum Growth Rate							
Mean	-162.05	101	86	1.00E-02	2	101	86
Max	-160.15	102	87	1.20E-02	2	109	86
Min	-133.14	96	85	3.40E-02	2	96	51.5

<b>QuadMean</b>	<b>-171.72</b>	<b>101</b>	<b>86</b>	<b>1.40E-02</b>	<b>1</b>	<b>101</b>	<b>86</b>
QuadMax	-162.42	102	87	1.10E-02	2	105.5	87
QuadMin	-133.65	96	85	1.80E-02	2	96	53

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**Appendix B-I Table B23:** Overall environmental model for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of ice-cover (ICE) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Final Environmental Model</b> (Number of observations 6769)							
<b>Group-Level</b>	<b>Effects:</b>						
~ID	(Number	of	levels:	1526)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	14.63	0.34	13.97	15.33	1	2406	4847
sd(Age)	1.82	0.06	1.7	1.94	1	3392	5955
cor(Intercept,Age)	0.8	0.02	0.75	0.84	1	2739	4521
~Year	(Number	of	levels:	27)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	11.63	1.85	8.59	15.84	1	2271	3617
sd(Age)	0.55	0.12	0.35	0.81	1	2449	4040
cor(Intercept,Age)	0.01	0.23	-0.43	0.45	1	4347	6159
<b>Population-Level</b>	<b>Effects:</b>						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	125.06	8.79	107.82	142.19	1	2385	4022
Age	6.98	0.97	5.07	8.88	1	2741	4956
SlopeWinICE	-0.63	18.47	-36.64	35.77	1	1802	3314
ISlopeWinICEE2	20.44	18.7	-15.78	57.17	1	1877	3566
IntWinTEMP	-0.68	0.35	-1.36	0	1	3415	5286
SlopeTEMPWin	0.92	0.46	0	1.82	1	2556	3904
<b>Age:SlopeWinICE</b>	<b>-3.01</b>	<b>2.56</b>	<b>-8.04</b>	<b>2.02</b>	1	2226	4883
<b>Age:ISlopeWinICEE2</b>	<b>6.51</b>	<b>2.52</b>	<b>1.55</b>	<b>11.48</b>	1	2332	5055
<b>Age:SlopeTEMPWin</b>	<b>0.2</b>	<b>0.05</b>	<b>0.11</b>	<b>0.29</b>	1	3739	5706
<b>Family</b>	<b>Specific Parameters</b>						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	12.33	0.14	12.06	12.6	1	4755	7096

**Appendix B-I Table B24:** Pre1995 environmental model for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of ice-cover (ICE) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Pre1995ICE</b>							
(Number of observations: 2057)							
Group-Level	Effects:						
~Band.No	(Number of levels: 454)						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	15.87	0.64	14.67	17.18	1	1007	1983
sd(Age)	1.97	0.11	1.76	2.2	1	1517	3121
cor(Intercept,Age)	0.81	0.03	0.73	0.87	1	1825	3100
~Year	(Number of levels: 9)						
	Estimate	Est.Error`	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	7.25	2.89	3.37	14.22	1	663	1621
sd(Age)	0.97	0.39	0.43	1.95	1	937	2097
cor(Intercept,Age)	0.35	0.35	-0.44	0.87	1	983	2331
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	262.86	62.22	145.26	384.56	1	418	1229
Age	34.52	9.5	16.58	53.03	1	495	1569
<b>IntWinICE</b>	<b>581.91</b>	<b>369.98</b>	<b>-141.76</b>	<b>1321.73</b>	1	588	1252
<b>IIntWinICEE2</b>	<b>-9775.08</b>	<b>4005.32</b>	<b>-17628.2</b>	<b>-1928.4</b>	1	665	1559
<b>SlopeWinICE</b>	<b>-395.28</b>	<b>184.57</b>	<b>-758.18</b>	<b>-43.65</b>	1	395	1087
<b>ISlopeWinICEE2</b>	<b>304.35</b>	<b>130.7</b>	<b>55.43</b>	<b>562.92</b>	1	391	1091
<b>Age:SlopeWinICE</b>	<b>-75.66</b>	<b>27.57</b>	<b>-129.94</b>	<b>-23.21</b>	1	475	1444
<b>Age:ISlopeWinICEE2</b>	<b>56.37</b>	<b>19.33</b>	<b>19.33</b>	<b>94.33</b>	1	473	1445
<b>Age:�ntWinICE</b>	<b>84.21</b>	<b>53.21</b>	<b>-18.86</b>	<b>188.54</b>	1	845	1695
<b>Age:�IntWinICEE2</b>	<b>-1614.07</b>	<b>590.3</b>	<b>-2775.21</b>	<b>-469.14</b>	1	934	1901
Family	Specific	Parameters:					
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	10.94	0.23	10.51	11.39	1	2632	5421

**Appendix B-I Table B25:** Post1995 environmental model for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of ice-cover (ICE) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Post1995ALL</b>							
(Number of observations: 4712)							
Group-Level Effects:							
~Band.No	(Number of levels: 1072)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	13.92	0.42	13.1	14.75	1	2957	5445
sd(Age)	1.71	0.08	1.57	1.87	1	3388	5879
cor(Intercept, Age)	0.79	0.03	0.72	0.85	1	3001	5295
~Year	(Number of levels: 18)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	8.85	2.11	5.58	13.74	1	2685	4792
sd(Age)	0.94	0.25	0.56	1.52	1	3142	5369
cor(Intercept, Age)	-0.2	0.28	-0.7	0.38	1	3094	5034
Population-Level Effects:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	132.77	12.54	108.56	157.09	1	2149	4162
Age	11.43	1.86	7.81	15.12	1	2975	5067
IntWinICE	-14.39	57.98	-130.71	96.15	1	2309	4353
IIntWinICEE2	99.25	106.88	-105.78	308.53	1	2173	4311
SlopeWinICE	17.92	11.3	-3.71	40.65	1	3008	4994
<b>IntWinTEMP</b>	<b>2.28</b>	<b>0.94</b>	<b>0.45</b>	<b>4.1</b>	1	2684	4778
<b>IIntWinTEMPE2</b>	<b>0.17</b>	<b>0.06</b>	<b>0.06</b>	<b>0.28</b>	1	2659	4587
SlopeTEMPWin	-0.01	1.85	-3.67	3.59	1	2128	3725
ISlopeTEMPWinE2	0.03	0.07	-0.1	0.16	1	2242	3558
Age: IntWinICE	1.18	6.57	-12.23	14.05	1	3125	4864
Age: IIntWinICEE2	12.08	14.81	-16.46	41.47	1	2717	4954
Age: IntWinTEMP	0.06	0.13	-0.21	0.31	1	3530	5515
Age: IIntWinTEMPE2	0	0.01	-0.02	0.02	1	3596	5853
<b>Age: SlopeTEMPWin</b>	<b>-0.39</b>	<b>0.28</b>	<b>-0.94</b>	<b>0.15</b>	1	2921	5372
<b>Age: ISlopeTEMPWinE2</b>	<b>0.02</b>	<b>0.01</b>	<b>0</b>	<b>0.04</b>	1	3012	5475
Family Specific Parameters:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	12.88	0.17	12.54	13.23	1	5157	6740

**Appendix B-I Table B26:** Pre1999 environmental model for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of ice-cover (ICE) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Pre1999AirTEMP</b>							
(Number of observations: 3616)							
Group-Level Effects:							
~Band.No	(Number of levels: 744)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	8.32	0.65	7.05	9.58	1	2819	4323
sd(Age)	1.81	0.08	1.65	1.97	1	1002	2245
cor(Intercept,Age)	-0.11	0.08	-0.27	0.06	1.01	504	858
~Year	(Number of levels: 13)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	5.09	1.47	2.96	8.72	1	3773	6534
sd(Age)	0.63	0.19	0.33	1.09	1	2654	5413
cor(Intercept,Age)	0.62	0.29	-0.08	0.98	1	3033	5315
Population-Level Effects:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	54.63	4.55	45.72	63.65	1	7909	8498
Age	11.71	0.74	10.27	13.16	1	3511	6007
<b>IntWinTEMP</b>	<b>-4.81</b>	<b>1.95</b>	<b>-8.73</b>	<b>-0.93</b>	<b>1</b>	3419	5200
<b>IIntWinTEMPE2</b>	<b>-0.22</b>	<b>0.07</b>	<b>-0.36</b>	<b>-0.08</b>	1	3494	5257
SlopeTEMPWin	2.51	2.07	-1.59	6.64	1	3300	5193
ISlopeTEMPWinE2	0.11	0.07	-0.03	0.26	1	3353	5302
Age:SlopeTEMPWin	-0.36	0.35	-1.04	0.32	1	2478	4342
Age:ISlopeTEMPWinE2	-0.01	0.01	-0.03	0.01	1	2457	4135
<b>Age:IntWinTEMP</b>	<b>0.77</b>	<b>0.32</b>	<b>0.15</b>	<b>1.4</b>	1	2503	4219
<b>Age:IIntWinTEMPE2</b>	<b>0.03</b>	<b>0.01</b>	<b>0.01</b>	<b>0.05</b>	1	2462	4342
Family Specific Parameters:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	11.36	0.17	11.03	11.7	1	4852	5864

**Appendix B-I Table B27:** Post1999 environmental model for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of ice-cover (ICE) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Post1999AirTEMP</b>							
(Number	of	observations:	3153)				
Group-Level							
~Band.No	(Number	of	levels:	782)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	13.89	0.5	12.93	14.88	1	2355	4012
sd(Age)	1.84	0.1	1.65	2.03	1	2754	4883
cor(Intercept, Age)	0.77	0.04	0.69	0.85	1	2133	3184
~Year	(Number	of	levels:	14)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	11.95	3.02	7.52	19.26	1	1687	3128
sd(Age)	0.75	0.23	0.4	1.3	1	2179	3389
cor(Intercept, Age)	-0.11	0.33	-0.72	0.54	1	2590	3903
Population-Level							
	Effects:						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	150.16	21.81	106.5	193.01	1	1464	3221
Age	9.38	3.56	2.36	16.42	1	1712	2767
<b>IntWinTEMP</b>	<b>2.08</b>	<b>1.2</b>	<b>-0.31</b>	<b>4.32</b>	1	1471	2997
<b>IIntWinTEMPE2</b>	<b>0.16</b>	<b>0.07</b>	<b>0.02</b>	<b>0.29</b>	1	1412	2930
SlopeTEMPWin	-2.08	3.6	-9.02	4.96	1	1401	3045
ISlopeTEMPWinE2	0.17	0.15	-0.13	0.47	1	1260	2737
Age:SlopeTEMPWin	0.04	0.59	-1.12	1.21	1	1619	2889
Age:ISlopeTEMPWinE2	0.01	0.03	-0.04	0.06	1	1611	2997
Age:IntWinTEMP	0.15	0.19	-0.24	0.52	1	1849	3733
Age:IIntWinTEMPE2	0.01	0.01	-0.02	0.03	1	1834	3763
Family	Specific	Parameters:					
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	13.46	0.23	13.02	13.92	1	3508	5242

**Appendix B-I Table B28:** Overall environmental models for gull growth. Two models are displayed as both had equal support in our model selection approach. The prefix *A* is used for the asymptote, *Ti* for the inflection point, *k* for the maximum growth rate, and *d* for the shape parameter. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>OverallSST Model</b>							
(Number of observations: 3221)	Effects:		levels: 1418)				
Group-Level ~ID	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	2.25	0.09	2.08	2.43	1	1089	2532
sd(k_Intercept)	0.68	0.04	0.59	0.77	1	1819	3342
sd(Ti_Intercept)	3.71	0.16	3.4	4.03	1	1156	2341
cor(A_Intercept,k_Intercept)	-0.42	0.07	-0.55	-0.27	1	1842	3467
cor(A_Intercept,Ti_Intercept)	0.69	0.03	0.61	0.75	1	1323	2113
cor(k_Intercept,Ti_Intercept)	-0.89	0.02	-0.93	-0.84	1	1877	3578
~Year (Number of observations: 12)	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.36	0.24	0.03	0.93	1	710	1868
sd(k_Intercept)	0.26	0.11	0.08	0.52	1	1929	2089
sd(Ti_Intercept)	1.06	0.42	0.4	2.06	1	1541	2941
cor(A_Intercept,k_Intercept)	-0.26	0.44	-0.92	0.69	1	1427	2626
cor(A_Intercept,Ti_Intercept)	0.04	0.46	-0.85	0.81	1	1213	2844
cor(k_Intercept,Ti_Intercept)	-0.25	0.38	-0.83	0.59	1	2231	4326
Population-Level	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.33	0.08	2.19	2.49	1	5122	6854
A_Intercept	8.95	0.99	6.99	10.88	1	19404	7209
A_A1WIN	-0.57	1.11	-2.78	1.61	1	1492	2804
A_IA1WINE2	0.01	0.08	-0.14	0.17	1	1625	3107
A_Ti1WIN	0.94	0.95	-0.91	2.81	1	1244	2947
A_ITi1WINE2	-0.04	0.04	-0.12	0.04	1	1274	3163
A_k1WIN	-1.19	1.9	-4.96	2.51	1	1074	2320
A_Ik1WINE2	0.13	0.16	-0.18	0.44	1	1097	2385
k_Intercept	5.35	0.9	3.58	7.1	1	17463	8018
k_A1WIN	0.53	0.47	-0.41	1.43	1	2156	4263
k_IA1WINE2	-0.04	0.03	-0.1	0.02	1	2203	4275
k_Ti1WIN	0.48	0.44	-0.36	1.36	1	2050	4437
k_ITi1WINE2	-0.02	0.02	-0.06	0.01	1	2089	4134
<b>k_k1WIN</b>	<b>-1.77</b>	<b>0.82</b>	<b>-3.39</b>	<b>-0.14</b>	1	2212	4188
<b>k_Ik1WINE2</b>	<b>0.15</b>	<b>0.07</b>	<b>0.02</b>	<b>0.28</b>	1	2227	4546
Ti_Intercept	15.48	1.99	11.51	19.33	1	17690	6972
Ti_A1WIN	-1.82	1.87	-5.48	1.86	1	1622	2954

Ti_IA1WINE2	0.16	0.13	-0.1	0.42	1	1748	3343
Ti_Ti1WIN	-2.49	1.59	-5.67	0.52	1	1508	2294
Ti_ITi1WINE2	0.08	0.07	-0.04	0.22	1	1471	2962
<b>Ti_k1WIN</b>	<b>7.98</b>	<b>3.13</b>	<b>2.06</b>	<b>14.45</b>	1	1579	3104
<b>Ti_Ik1WINE2</b>	<b>-0.67</b>	<b>0.26</b>	<b>-1.21</b>	<b>-0.18</b>	1	1614	3154
<b>OverallALL Effects Model</b>							
(Number of observations: 3221)							
Group-Level Effects:							
~ID (Number of levels: 1418)							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	2.24	0.09	2.07	2.42	1	1738	3348
sd(k_Intercept)	0.69	0.04	0.6	0.77	1	2431	4445
sd(Ti_Intercept)	3.75	0.16	3.45	4.08	1	1878	3607
cor(A_Intercept,k_Intercept)	-0.42	0.07	-0.55	-0.27	1	2495	5034
cor(A_Intercept,Ti_Intercept)	0.68	0.03	0.61	0.75	1	1729	3331
cor(k_Intercept,Ti_Intercept)	-0.89	0.02	-0.94	-0.84	1	2168	3509
~Year (Number of levels: 12)							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.21	0.17	0.01	0.63	1.01	975	2583
sd(k_Intercept)	0.33	0.11	0.17	0.58	1	5101	6876
sd(Ti_Intercept)	0.9	0.33	0.36	1.68	1	2510	3063
cor(A_Intercept,k_Intercept)	0.01	0.47	-0.84	0.86	1	1433	3562
cor(A_Intercept,Ti_Intercept)	-0.04	0.47	-0.87	0.82	1	1815	3748
cor(k_Intercept,Ti_Intercept)	-0.42	0.32	-0.87	0.32	1	4666	6141
Population-Level Effects:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.35	0.08	2.2	2.5	1	7286	7943
A_Intercept	9.59	0.91	7.82	11.36	1	5565	7089
<b>A_A1WINTEMP</b>	<b>-2.46</b>	<b>0.96</b>	<b>-4.34</b>	<b>-0.59</b>	1	1366	2932
A_Ti1WINTEMP	0.54	0.3	-0.06	1.12	1	1650	2943
A_ITi1WINTEMPE2	-0.03	0.02	-0.06	0	1	1823	2976
k_Intercept	3.76	0.79	2.18	5.31	1	8464	7414
k_k1WIN	0.33	0.28	-0.21	0.87	1	6753	6847
k_Ik1WINE2	-0.03	0.03	-0.08	0.02	1	5997	6603
Ti_Intercept	13.17	1.89	9.44	16.85	1	14311	6971
Ti_A1WINTEMP	-0.3	1.17	-2.63	1.99	1	2237	4432
<b>Ti_Ti1WINTEMP</b>	<b>1.49</b>	<b>0.51</b>	<b>0.49</b>	<b>2.48</b>	1	3714	5428
<b>Ti_ITi1WINTEMPE2</b>	<b>-0.07</b>	<b>0.03</b>	<b>-0.13</b>	<b>-0.02</b>	1	3866	5654
Ti_k1WIN	-0.97	0.94	-2.78	0.91	1	6020	7542
Ti_Ik1WINE2	0.05	0.08	-0.11	0.21	1	5852	7274
Family Specific Parameters:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	35.06	0.64	33.85	36.34	1	3352	6511

**Appendix B-I Table B29:** Pre2009 environmental models for gull growth. The prefix *A* is used for the asymptote, *Ti* for the inflection point, *k* for the maximum growth rate, and *d* for the shape parameter. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Pre2009SST Model</b>							
(Number of observations: 1512)							
Group-Level	Effects:						
~ID	(Number of levels: 670)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	2.12	0.16	1.81	2.45	1	1688	3110
sd(k_Intercept)	0.62	0.06	0.5	0.73	1	1426	3199
sd(Ti_Intercept)	3.56	0.24	3.13	4.05	1	1813	3844
cor(A_Intercept,k_Intercept)	-0.19	0.12	-0.42	0.07	1	2540	4654
cor(A_Intercept,Ti_Intercept)	0.56	0.07	0.41	0.68	1	1925	4065
cor(k_Intercept,Ti_Intercept)	-0.86	0.04	-0.93	-0.76	1	2157	3350
~Year	(Number of levels: 7)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.57	0.51	0.02	1.88	1	2279	5197
sd(k_Intercept)	0.11	0.1	0	0.37	1	6120	6252
sd(Ti_Intercept)	1.19	0.77	0.18	3.15	1	2914	2711
cor(A_Intercept,k_Intercept)	-0.05	0.5	-0.9	0.87	1	12898	7624
cor(A_Intercept,Ti_Intercept)	0.01	0.49	-0.87	0.85	1	4732	6830
cor(k_Intercept,Ti_Intercept)	-0.06	0.51	-0.91	0.87	1	5396	7253
Population-Level	Effects:						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.2	0.1	2.01	2.4	1	7950	8433
A_Intercept	9.47	0.99	7.55	11.39	1	25697	6648
A_A1WIN	-1.27	2.51	-6.29	3.53	1	3969	5734
A_IA1WINE2	0.14	0.23	-0.3	0.59	1	3843	5545
A_Ti1WIN	1.02	3.05	-4.95	7.02	1	3799	4907
A_ITi1WINE2	-0.11	0.25	-0.61	0.39	1	3723	4941
A_k1WIN	0.03	1.95	-3.78	3.92	1	2683	4480
A_Ik1WINE2	0	0.15	-0.3	0.29	1	2986	4164
k_Intercept	4.81	0.85	3.17	6.49	1	18768	7928
<b>k_A1WIN</b>	<b>1.59</b>	<b>0.95</b>	<b>-0.3</b>	<b>3.47</b>	1	4142	6107
<b>k_IA1WINE2</b>	<b>-0.2</b>	<b>0.09</b>	<b>-0.37</b>	<b>-0.03</b>	1	4192	5945
k_Ti1WIN	-1.17	1.22	-3.53	1.22	1	3511	5619
k_ITi1WINE2	0.12	0.1	-0.08	0.31	1	3484	5310
k_k1WIN	-0.05	0.68	-1.38	1.26	1	3935	5847
k_Ik1WINE2	-0.01	0.05	-0.11	0.09	1	3906	5785
Ti_Intercept	13.92	1.98	10.04	17.68	1	24187	7110
Ti_A1WIN	-0.98	3.08	-7.02	5.12	1	4402	6425
Ti_IA1WINE2	0.3	0.3	-0.3	0.89	1	4457	6394
Ti_Ti1WIN	0.84	3.56	-6.06	7.96	1	4117	6220
Ti_ITi1WINE2	-0.33	0.32	-0.95	0.29	1	3770	5800
Ti_k1WIN	-0.45	2.59	-5.56	4.73	1	3502	5390
Ti_Ik1WINE2	0.22	0.21	-0.19	0.63	1	3556	5280
Family	Specific	Parameters:					

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<u>sigma</u>	34.66	0.87	32.98	36.37	1	2767	6078

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**Appendix B-I Table B30:** Post2009 environmental models for gull growth. The prefix *A* is used for the asymptote, *Ti* for the inflection point, *k* for the maximum growth rate, and *d* for the shape parameter. Standard error and 95% highest posterior density intervals are shown. All non-intercept terms had CIs that overlap zero. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

Post 2009SST Model	(Number	of	observations:	1709)			
Group-Level	Effects:						
~ID	(Number	of	levels:	748)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	2.27	0.11	2.07	2.5	1	1171	2014
sd(k_Intercept)	0.7	0.06	0.59	0.81	1	1637	4230
sd(Ti_Intercept)	3.72	0.2	3.34	4.13	1	1283	2622
cor(A_Intercept,k_Intercept)	-0.54	0.08	-0.69	-0.36	1	2086	3936
cor(A_Intercept,Ti_Intercept)	0.73	0.04	0.65	0.79	1	1366	2344
cor(k_Intercept,Ti_Intercept)	-0.92	0.03	-0.97	-0.86	1	1201	2125
~Year	(Number	of	levels:	5)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.94	1.11	0.03	3.28	1	1042	2892
sd(k_Intercept)	0.34	0.39	0.01	1.29	1	2310	4597
sd(Ti_Intercept)	1.19	1.06	0.07	3.92	1	1265	2789
cor(A_Intercept,k_Intercept)	0.09	0.51	-0.86	0.91	1	5090	6420
cor(A_Intercept,Ti_Intercept)	0.28	0.49	-0.76	0.96	1	2801	5590
cor(k_Intercept,Ti_Intercept)	-0.19	0.5	-0.94	0.81	1	5447	6720
Population-Level	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.5	0.12	2.28	2.73	1	5521	7305
A_Intercept	9.08	1	7.12	11.05	1	16019	6882
A_A1WIN	-0.59	1.33	-3.24	2.01	1	1435	2639
A_IA1WINE2	0.02	0.05	-0.08	0.11	1	1421	2525
A_Ti1WIN	1.49	5.01	-8.1	11.74	1	5901	6263
A_ITi1WINE2	-2.02	1.86	-5.8	1.58	1	3432	5541
A_k1WIN	1.65	2.97	-3.98	7.66	1	1283	2389
A_Ik1WINE2	-0.1	0.25	-0.6	0.39	1	1290	2349
k_Intercept	4.98	0.91	3.22	6.76	1	17286	7599
k_A1WIN	-1.05	0.79	-2.64	0.44	1	2459	3753
k_IA1WINE2	0.03	0.03	-0.02	0.09	1	2492	3854
k_Ti1WIN	6.58	5.08	-2.84	17.41	1	3697	4416
k_ITi1WINE2	-2.04	1.81	-5.86	1.31	1	3887	4738
k_k1WIN	0.87	1.55	-1.98	4.12	1	2093	3193
k_Ik1WINE2	-0.07	0.13	-0.34	0.18	1	2084	3601
Ti_Intercept	15.03	2.01	11.11	19.03	1	15915	7939
Ti_A1WIN	2.64	1.8	-0.79	6.34	1	1870	2969
Ti_IA1WINE2	-0.09	0.07	-0.22	0.04	1	1827	3129
Ti_Ti1WIN	0.43	4.86	-9.2	10.23	1	7213	7212
Ti_ITi1WINE2	-1.59	2.07	-5.74	2.5	1	2840	5679
Ti_k1WIN	-5.73	3.97	-13.94	1.74	1	1842	3153
Ti_Ik1WINE2	0.47	0.34	-0.18	1.17	1	1762	2920
sigma	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
	35.33	0.87	33.66	37.09	1	2939	5758

**Appendix B-I Table B31:** Overall environmental models for second-hatched kittiwake growth. The prefix *A* is used for the asymptote, *Ti* for the inflection point, *k* for the maximum growth rate, and *d* for the shape parameter. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>BetaAirTEMP</b>	(Number	of	observations:	3522)			
Group-Level	(Number	of	levels:	788)			
~ChickID	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.42	0.02	0.38	0.47	1	2152	4064
sd(k_Intercept)	0.53	0.04	0.46	0.6	1	3329	5487
sd(Ti_Intercept)	1.96	0.11	1.76	2.18	1	1909	3389
cor(A_Intercept,k_Intercept)	-0.17	0.09	-0.34	0.02	1	2239	4471
cor(A_Intercept,Ti_Intercept)	0.46	0.06	0.34	0.56	1	1793	3922
cor(k_Intercept,Ti_Intercept)	-0.94	0.02	-0.98	-0.88	1	1777	3277
~Year	(Number	of	levels:	21)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.28	0.08	0.14	0.46	1	1724	2879
sd(k_Intercept)	0.22	0.08	0.06	0.39	1	1655	1914
sd(Ti_Intercept)	0.71	0.29	0.21	1.35	1	985	1178
cor(A_Intercept,k_Intercept)	-0.03	0.37	-0.7	0.67	1	2610	4411
cor(A_Intercept,Ti_Intercept)	0.34	0.37	-0.53	0.85	1	1615	2811
cor(k_Intercept,Ti_Intercept)	-0.49	0.34	-0.91	0.4	1	1672	2148
Population-Level	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	1.9	0.05	1.8	2.01	1	13951	7443
A_Intercept	4.64	0.86	2.96	6.29	1	4805	6506
A_A1WINTEMP	0.32	1.54	-2.67	3.32	1	4178	5406
A_IA1WINTEMPE2	-0.6	0.76	-2.08	0.89	1	3228	5104
<b>A_Ti1WINTEMP</b>	<b>-0.24</b>	<b>0.22</b>	<b>-0.66</b>	<b>0.21</b>	1	2906	4472
<b>A_ITi1WINTEMPE2</b>	<b>-1.16</b>	<b>0.36</b>	<b>-1.89</b>	<b>-0.49</b>	1	2119	3720
k_Intercept	4.86	0.81	3.27	6.46	1	6373	6493
k_A1WINTEMP	-0.08	1.46	-2.88	2.84	1	5160	6043
k_IA1WINTEMPE2	0.12	0.76	-1.4	1.61	1	4040	6097
<b>k_Ti1WINTEMP</b>	<b>-0.59</b>	<b>0.2</b>	<b>-0.95</b>	<b>-0.15</b>	1	3594	5022
<b>k_ITi1WINTEMPE2</b>	<b>-1.06</b>	<b>0.34</b>	<b>-1.68</b>	<b>-0.34</b>	1	2344	4317
Ti_Intercept	14.47	1.62	11.3	17.61	1	8280	7583
Ti_A1WINTEMP	-2.1	2.91	-7.8	3.63	1	5865	6568
Ti_IA1WINTEMPE2	-0.31	1.8	-3.78	3.29	1	3048	4849
<b>Ti_Ti1WINTEMP</b>	<b>1.42</b>	<b>0.66</b>	<b>0.05</b>	<b>2.62</b>	1	2866	4229
<b>Ti_ITi1WINTEMPE2</b>	<b>2.04</b>	<b>1.35</b>	<b>-0.75</b>	<b>4.55</b>	1	1667	3425
Family	Specific	Parameters:					
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	19.7	0.28	19.17	20.25	1	8675	6928

**Appendix B-I Table B32:** Pre2008 environmental models for second-hatched kittiwake growth. Two models are displayed as both had equal support in our model selection approach. The prefix *A* is used for the asymptote, *Ti* for the inflection point, *k* for the maximum growth rate, and *d* for the shape parameter. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Pre2008BetaSST</b>							
(Number of observations: 1674)							
Group-Level Effects:							
~ChickID	(Number of levels: 332)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.47	0.03	0.41	0.53	1	2126	4195
sd(k_Intercept)	0.48	0.06	0.37	0.6	1	4579	6854
sd(Ti_Intercept)	1.88	0.14	1.61	2.17	1	2466	4790
cor(A_Intercept,k_Intercept)	-0.4	0.13	-0.63	-0.11	1	4164	6719
cor(A_Intercept,Ti_Intercept)	0.49	0.07	0.34	0.63	1	2519	4493
cor(k_Intercept,Ti_Intercept)	-0.96	0.03	-1	-0.89	1	1019	2946
~Year	(Number of levels: 10)						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.09	0.09	0	0.33	1	1080	1926
sd(k_Intercept)	0.26	0.13	0.04	0.57	1	2390	2117
sd(Ti_Intercept)	0.78	0.36	0.18	1.63	1	1760	1540
cor(A_Intercept,k_Intercept)	0.01	0.49	-0.86	0.88	1	2389	4374
cor(A_Intercept,Ti_Intercept)	0.01	0.49	-0.87	0.86	1	2282	4291
cor(k_Intercept,Ti_Intercept)	-0.66	0.32	-0.98	0.2	1	3285	4449
Population-Level Effects:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.09	0.08	1.94	2.25	1	17255	7629
A_Intercept	4.28	1.01	2.3	6.24	1	21832	6723
A_A1WIN	-1.04	1.18	-3.39	1.29	1	1717	3050
A_IA1WINE2	0.03	0.04	-0.06	0.12	1	1749	3082
A_Ti1WIN	1.23	1.22	-1.18	3.65	1	1712	2951
A_ITi1WINE2	-0.05	0.05	-0.14	0.05	1	1754	3047
k_Intercept	5.02	0.91	3.24	6.82	1	21051	6389
k_A1WIN	1.68	1.4	-1.06	4.47	1	2876	4767
k_IA1WINE2	-0.05	0.05	-0.15	0.05	1	2905	4779
k_Ti1WIN	-1.45	1.44	-4.35	1.37	1	2862	4799
k_ITi1WINE2	0.03	0.05	-0.07	0.14	1	2871	4675
Ti_Intercept	15	1.94	11.2	18.85	1	20910	7290
Ti_A1WIN	1.21	2.97	-4.5	7.2	1	2663	4133
Ti_IA1WINE2	-0.05	0.11	-0.27	0.16	1	2699	4237
Ti_Ti1WIN	-2.51	3.09	-8.79	3.44	1	2696	4085

Ti_ITi1WINE2	0.13	0.12	-0.09	0.37	1	2760	4231
Family	Specific	Parameters:					
sigma	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
	20.36	0.41	19.59	21.17	1	9240	7594

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**Pre2008AirTEMP**

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(Number	of	observations:	1674)				
Group-Level	Effects:						
~ChickID	(Number	of	levels:	332)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.47	0.03	0.41	0.53	1	2801	5539
sd(k_Intercept)	0.47	0.06	0.36	0.59	1	5235	7422
sd(Ti_Intercept)	1.87	0.15	1.61	2.17	1	2947	5320
cor(A_Intercept,k_Intercept)	-0.43	0.14	-0.67	-0.14	1	5099	7736
cor(A_Intercept,Ti_Intercept)	0.5	0.08	0.34	0.64	1	3462	5371
cor(k_Intercept,Ti_Intercept)	-0.96	0.03	-1	-0.88	1	887	2454

~Year	(Number	of	levels:	10)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.12	0.1	0	0.37	1	1382	2786
sd(k_Intercept)	0.15	0.13	0.01	0.47	1	2361	4093
sd(Ti_Intercept)	0.47	0.38	0.02	1.43	1	1664	3911
cor(A_Intercept,k_Intercept)	0.11	0.51	-0.86	0.92	1	6662	6422
cor(A_Intercept,Ti_Intercept)	-0.02	0.5	-0.88	0.87	1	5846	6834
cor(k_Intercept,Ti_Intercept)	-0.33	0.51	-0.97	0.78	1	2784	5770

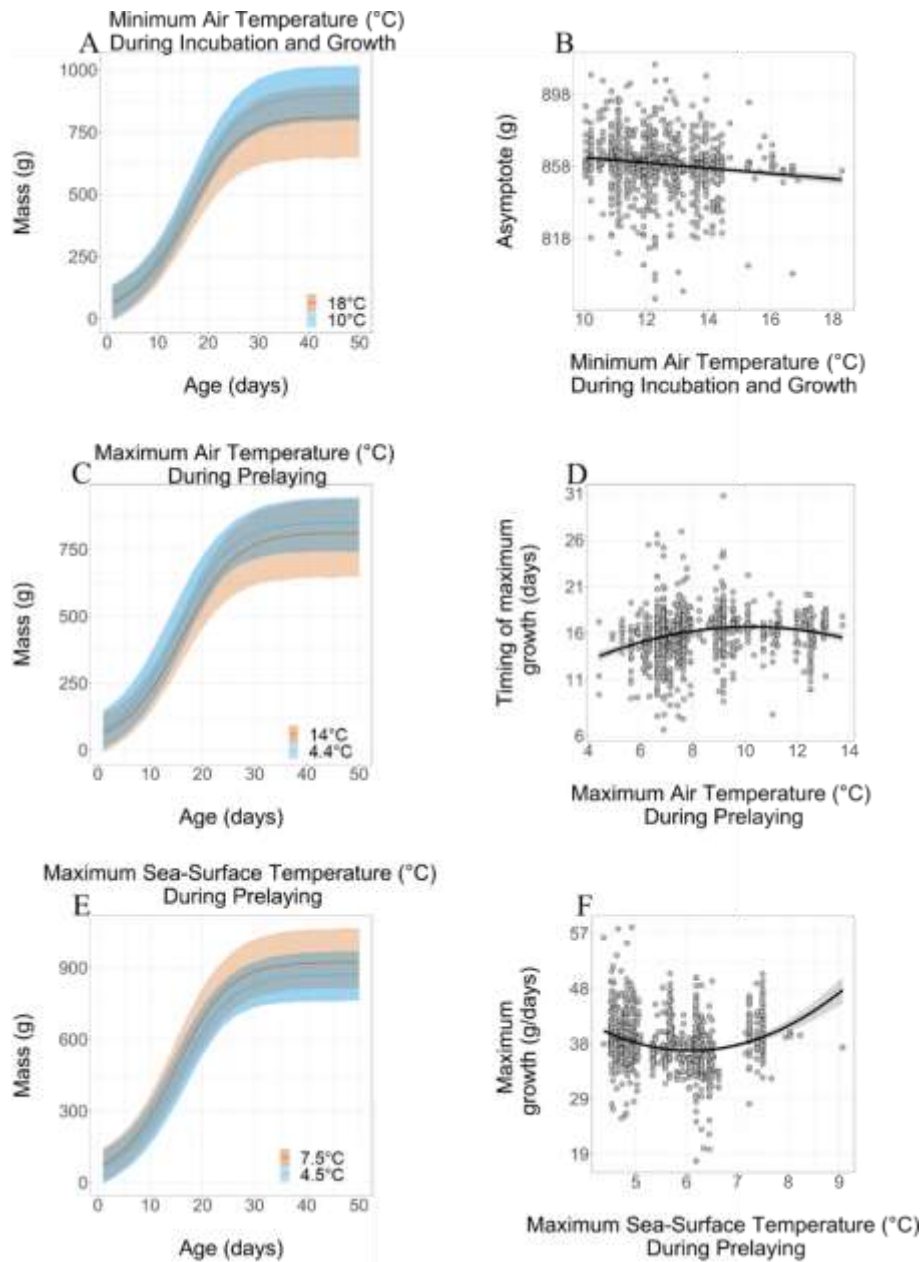
Population-Level	Effects:						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	2.1	0.08	1.94	2.26	1	19514	7532
A_Intercept	4.75	0.96	2.87	6.62	1	8391	7656
A_A1WINTEMP	-0.03	0.17	-0.35	0.3	1	5955	7095
A_IA1WINTEMPE2	0	0.01	-0.02	0.01	1	3408	4735
A_Ti1WINTEMP	0.01	0.02	-0.03	0.05	1	1281	1555
A_ITi1WINTEMPE2	0	0	-0.01	0.01	1	1712	2934
k_Intercept	4.96	0.88	3.24	6.72	1	12306	7657
k_A1WINTEMP	-0.02	0.16	-0.34	0.3	1	6281	7263
k_IA1WINTEMPE2	0.01	0.01	-0.01	0.02	1	3889	5317
k_Ti1WINTEMP	-0.04	0.03	-0.09	0.02	1	2902	3638
<b>k_ITi1WINTEMPE2</b>	<b>-0.03</b>	<b>0.01</b>	<b>-0.04</b>	<b>-0.01</b>	1	3263	5100
Ti_Intercept	15.16	1.98	11.3	19.04	1	14075	7604
Ti_A1WINTEMP	-0.62	0.42	-1.44	0.17	1	5494	6954
Ti_IA1WINTEMPE2	0.03	0.03	-0.03	0.08	1	3384	4707
Ti_Ti1WINTEMP	0.12	0.08	-0.05	0.26	1	2054	3431
<b>Ti_ITi1WINTEMPE2</b>	<b>0.05</b>	<b>0.02</b>	<b>0.02</b>	<b>0.08</b>	1	2163	4051

Family	Specific	Parameters:					
sigma	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
	20.36	0.41	19.57	21.18	1	10545	7449

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**Appendix B-I Table B33:** Post 2008 environmental models for second-hatched kittiwake growth. The prefix A is used for the asymptote, Ti for the inflection point, k for the maximum growth rate, and d for the shape parameter. Standard error and 95% highest posterior density intervals are shown. All non-intercept terms had CIs that overlap zero. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface (SST) or air temperature (TEMP). The effect of a quadratic term is indicated by E2.

<b>Post2008BetaSST</b>		(Number of observations: 1848)					
Group-Level	Effects:						
~ChickID	(Number	of	levels:	456)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.42	0.03	0.36	0.49	1	2348	4644
sd(k_Intercept)	0.57	0.05	0.48	0.66	1	3262	6237
sd(Ti_Intercept)	2.09	0.16	1.79	2.41	1	1636	2970
cor(A_Intercept,k_Intercept)	-0.1	0.12	-0.33	0.16	1	1763	3482
cor(A_Intercept,Ti_Intercept)	0.41	0.08	0.23	0.56	1	1730	3690
cor(k_Intercept,Ti_Intercept)	-0.92	0.03	-0.97	-0.84	1	1789	4517
~Year	(Number	of	levels:	11)			
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(A_Intercept)	0.5	0.17	0.26	0.9	1	3942	6044
sd(k_Intercept)	0.19	0.12	0.01	0.47	1	1899	2330
sd(Ti_Intercept)	0.99	0.44	0.35	2.05	1	2044	3645
cor(A_Intercept,k_Intercept)	0.32	0.42	-0.61	0.93	1	5567	6050
cor(A_Intercept,Ti_Intercept)	0.1	0.38	-0.68	0.74	1	4299	5395
cor(k_Intercept,Ti_Intercept)	-0.43	0.42	-0.95	0.6	1	2407	2953
Population-Level	Effects:						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
d_Intercept	1.78	0.07	1.65	1.91	1	16341	7936
A_Intercept	3.72	0.87	2.01	5.42	1	9689	7598
A_A1WIN	-0.12	0.4	-0.91	0.67	1	1881	3146
A_IA1WINE2	0	0.02	-0.04	0.04	1	1942	3274
A_Ti1WIN	0.31	0.52	-0.7	1.33	1	2074	3520
A_ITi1WINE2	-0.02	0.03	-0.08	0.05	1	2136	4040
k_Intercept	5.44	0.78	3.9	6.97	1	13730	7726
k_A1WIN	0.35	0.39	-0.4	1.13	1	2408	3331
k_IA1WINE2	-0.02	0.02	-0.06	0.02	1	2450	3509
k_Ti1WIN	-0.6	0.47	-1.53	0.31	1	2351	3674
k_ITi1WINE2	0.02	0.03	-0.03	0.08	1	2348	3491
Ti_Intercept	15.08	1.87	11.38	18.71	1	16927	7248
Ti_A1WIN	-1.3	1.35	-3.98	1.31	1	1854	3255
Ti_IA1WINE2	0.04	0.07	-0.09	0.19	1	1904	3625
Ti_Ti1WIN	0.82	1.7	-2.44	4.27	1	1924	3380
Ti_ITi1WINE2	0.01	0.11	-0.22	0.22	1	1990	3271
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	19.13	0.38	18.39	19.88	1	6645	7466



**Appendix B-I Figure B1:** Environmental effects on glaucous-winged gull growth. Model predicted effects of A) maximum air temperature during early growth and incubation (10°C versus 18°C), and B) maximum air temperature during mid to late growth (4°C versus 13°C) periods identified by our sliding window analysis on the growth of **glaucous-winged gull** nestlings.

## APPENDIX B-II: SEA-SURFACE TEMPERATURE ANALYSIS FOR MURRES

**Appendix B-II Table B1:** Comparison of the leave one out cross-validation information criterion (LOOIC) for competing models for each murre across the entire dataset and split before and after 1999. Delta LOOIC ( $\Delta$ LOOIC) is the LOOIC value of each model subtract the highest LOOIC in each species/data subset comparison.  $\Delta$ LOOIC values are displayed with the ascending order. Bolded values indicate models that are the lowest in a particular comparison and are within 5  $\Delta$ LOOIC of each other. Names of the models indicate the environmental windows included as predictors in that particular model. "Base" is the baseline model without any predictors, "Ice-cover" is a model with only ice-cover windows as predictors, "Air temp" is the model with only air temperature windows as predictors, and SST is a model with only sea-surface temperature windows as predictors. "All windows" is a model that included all effects from ice-cover, sea-surface temperature and air temperature models with posterior distributions that did not overlap zero.

Overall Model	$\Delta$ LOOIC	PreModel	$\Delta$ LOOIC	PostModel	$\Delta$ LOOIC
<b>Murres</b>					
<b>SST</b>	<b>-108.3</b>	<b>Air Temp</b>	<b>-105.9</b>	<b>All windows</b>	<b>-23.9</b>
Ice cover	-77.2	<b>All windows</b>	<b>-104.9</b>	SST	-17.8
Air temp	-94.9	SST	-101.8	Air Temp	-17.6
All windows	-71.9	Ice cover	-87.9	Base	-14.7
Base	0	Base	0	Ice cover	0

**Appendix B-II Table B2:** Comparison of the leave one out cross-validation information criterion (LOOIC) for competing models for each murre across the entire dataset and split before and after 1994. Delta LOOIC ( $\Delta$ LOOIC) is the LOOIC value of each model subtract the highest LOOIC in each species/data subset comparison.  $\Delta$ LOOIC values are displayed with the ascending order. Bolded values indicate models that are the lowest in a particular comparison and are within 5  $\Delta$ LOOIC of each other. Names of the models indicate the environmental windows included as predictors in that particular model. "Base" is the baseline model without any predictors, "Ice-cover" is a model with only ice-cover windows as predictors, "Air temp" is the model with only air temperature windows as predictors, and SST is a model with only sea-surface temperature windows as predictors. "All windows" is a model that included all effects from ice-cover, sea-surface temperature and air temperature models with posterior distributions that did not overlap zero.

Overall Model	$\Delta$ LOOIC	PreModel	$\Delta$ LOOIC	PostModel	$\Delta$ LOOIC
<b>Murres</b>					
<b>SST</b>	<b>-108.3</b>	<b>Ice cover</b>	<b>-13.4</b>	Air Temp	<b>-101.3</b>
Ice cover	-77.2	<b>All windows</b>	<b>-11.9</b>	Ice cover	<b>-100.0</b>
Air temp	-94.9	Air Temp	-5.1	All windows	<b>-98.8</b>
All windows	-71.9	SST	-4.3	SST	<b>-99.3</b>
Base	0	Base	0	Base	0

**Appendix B-II Table B3:** Results of overall murre climwin analysis for sea-surface temperature. The best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

Overall	Murre	SST						
Intercept								
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Mean	-141.217	7	4	1.00E-03	1	7	4	
Max	-141.217	31	9	1.00E-03	6	61	8	
Min	-139.113	7	5	1.00E-03	1	7	5	
QuadMean	-153.636	7	5	3.00E-03	1	7	5	
<b>QuadMax</b>	<b>-168.942</b>	<b>30</b>	<b>8</b>	<b>1.00E-03</b>	<b>5</b>	<b>60</b>	<b>8</b>	
QuadMin	-153.63	7	7	1.00E-03	1	7	5	
Slope								
Mean	-109.914	82	68	1.00E-03	3	82	66	
Max	-108.201	79	77	1.00E-03	1	80	77.5	
<b>Min</b>	<b>-117.767</b>	<b>76</b>	<b>69</b>	<b>1.00E-03</b>	<b>1</b>	<b>78</b>	<b>68</b>	
QuadMean	-110.427	80	56	1.00E-03	7	81	55	
QuadMax	-106.929	79	78	1.00E-03	2	78	61	
QuadMin	-116.595	78	69	1.00E-03	1	78	68	

**Appendix B-II Table B4:** Results of pre1995 murre climwin analysis for sea-surface temperature. The best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

Pre1995	Murre	SST						
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Intercept								
Mean	-17.0763	58	57	1.70E-02	8	72	57	
Max	-18.4414	58	57	2.20E-02	12	79	61	
Min	-18.3785	57	52	3.20E-02	17	64	33	
<b>QuadMean</b>	<b>-38.5001</b>	<b>14</b>	<b>14</b>	<b>1.30E-02</b>	<b>3</b>	<b>23</b>	<b>12</b>	
QuadMax	-38.5001	14	14	1.72E-01	10	60	15	
QuadMin	-39.5942	15	14	1.40E-02	2	17	<b>8</b>	
Slope								
Mean	-20.7451	68	66	2.20E-02	10	78	63	
Max	-20.3504	67	67	2.30E-02	16	78	63	
<b>Min</b>	<b>-24.7986</b>	<b>67</b>	<b>65</b>	<b>2.90E-02</b>	<b>19</b>	<b>72</b>	<b>37</b>	
QuadMean	-21.1138	69	64	3.20E-02	21	80	53	
QuadMax	-21.3999	79	77	6.20E-02	27	72	18	
QuadMin	-26.278	67	65	5.00E-02	24	73	40	

**Appendix B-II Table B5:** Results of post1995 murre climwin analysis for sea-surface temperature. The best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta$ AIC), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

Post1995	Murre	SST							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close		
Intercept									
Mean	-190.588	82	78	3.00E-03	1	81	78		
<b>Max</b>	<b>-200.116</b>	<b>82</b>	<b>78</b>	<b>2.00E-03</b>	<b>1</b>	<b>81.5</b>	<b>78.5</b>		
Min	-186.685	79	79	3.00E-03	1	79.5	79.5		
QuadMean	-189.438	82	78	3.00E-03	1	81	78		
QuadMax	-201.835	82	78	1.00E-02	1	81.5	78.5		
QuadMin	-186.662	80	80	4.00E-03	1	80	80		
Slope									
Mean	-95.2259	83	69	3.00E-03	4	84	64		
Max	-96.5941	81	78	2.00E-03	1	81.5	78		
Min	-99.1124	78	69	3.00E-03	2	79	66		
QuadMean	<b>-117.402</b>	<b>82</b>	<b>40</b>	<b>3.00E-03</b>	<b>2</b>	<b>82</b>	<b>40</b>		
QuadMax	-115.407	74	57	4.40E-02	2	76	57		
QuadMin	-100.726	49	38	0.004	2	40	29.5		

**Appendix B-II Table B6:** Results of pre1999 murre climwin analysis for sea-surface temperature. The best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

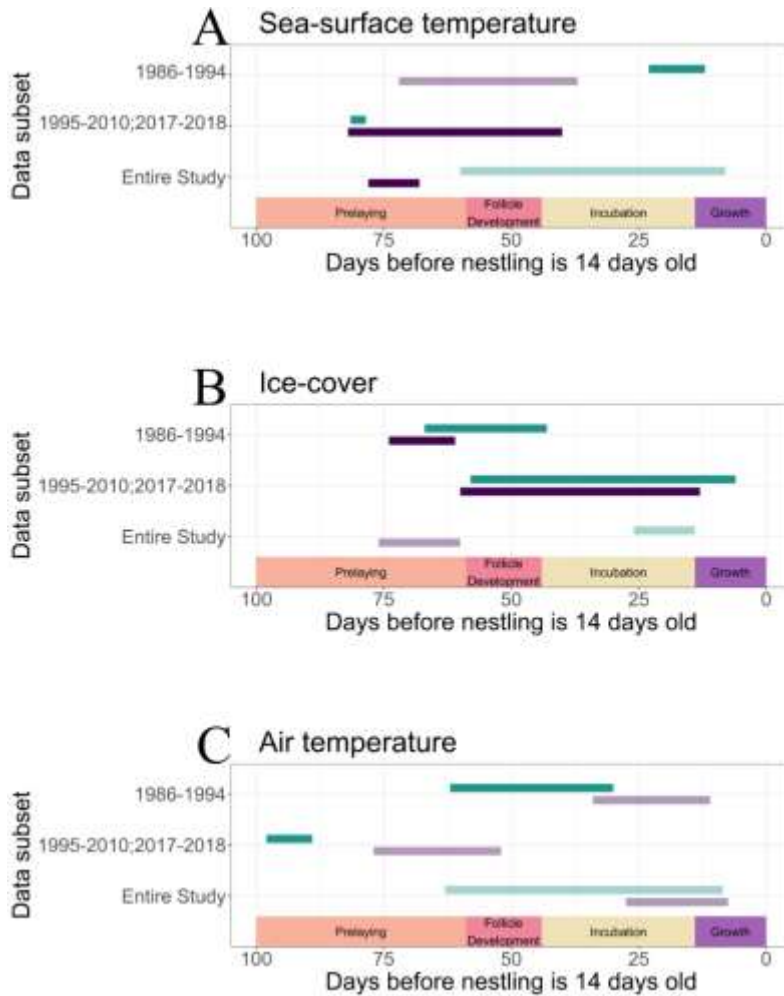
Pre1999	Murre	SST						
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close	
Intercept								
Mean	-28.9076	58	56	2.10E-02	23	80	46	
Max	-31.5803	44	42	1.30E-02	10	76	41	
Min	-37.2071	76	69	1.80E-02	19	77	34	
QuadMean	-77.9621	19	7	8.00E-03	2	19	7	
<b>QuadMax</b>	<b>-94.518</b>	<b>17</b>	<b>13</b>	<b>1.00E-02</b>	<b>5</b>	<b>54.5</b>	<b>13</b>	
QuadMin	-76.9394	12	9	9.00E-03	1	12	9	
Slope								
Mean	-51.7244	70	69	9.00E-03	1	12	9	
Max	-51.2004	69	69	9.00E-03	3	79	73	
Min	-57.4853	76	69	1.00E-02	10	79	42	
<b>QuadMean</b>	<b>-57.2885</b>	<b>70</b>	<b>65</b>	<b>1.40E-02</b>	<b>13</b>	<b>79</b>	<b>51</b>	
QuadMax	-55.1313	69	69	1.80E-02	7	80	66	
QuadMin	-57.7443	70	69	1.90E-02	6	76	61	

**Appendix B-II Table B7:** Results of pre1999 murre climwin analysis for sea-surface temperature. The best models multiple summary statistics are reported: **1)** the difference between the Akaike Information Criterion of a model and that of a model with an intercept only ( $\Delta AIC$ ), **2)** the environmental window for each model is given by the beginning of the window (BestModel Open) and end of the window (Best Model Close) in days before the date a nestling was 14 days old, **3)** the probability of detecting a window just by chance (Pc), and **4)** the extent to which several windows have similar explanatory power as the top model (%Confidence). For each grouping the top models are displayed for all growth parameters extracted from our initial growth models (Intercept, Slope).

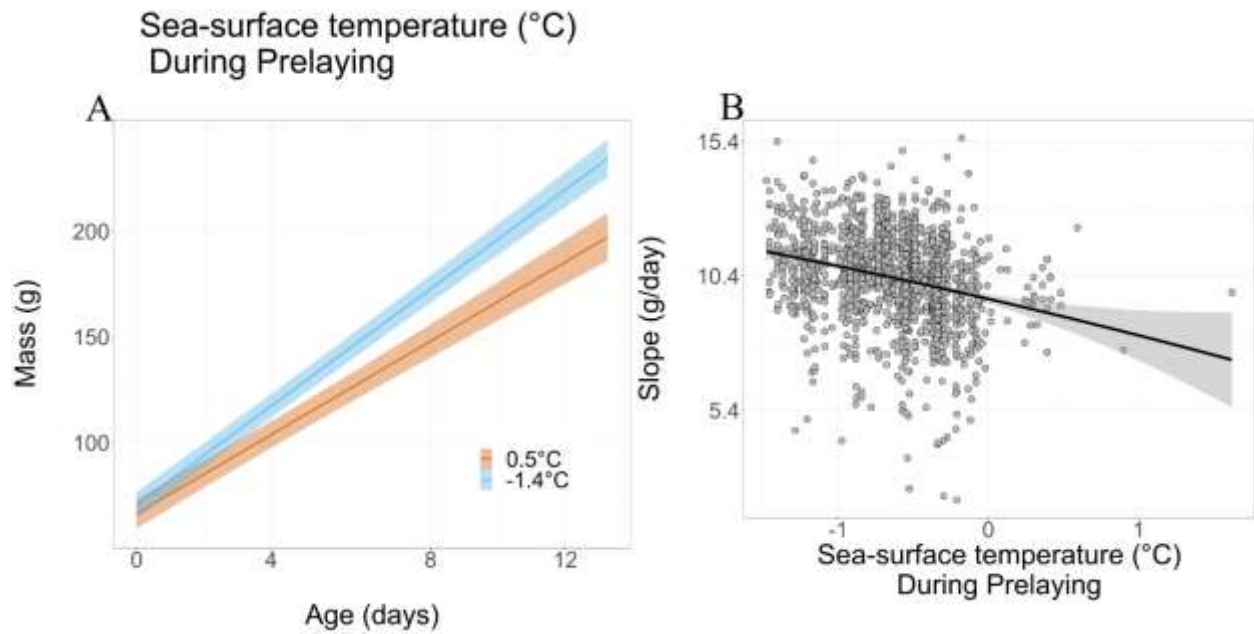
Post1999	Murre	SST							
Model	deltaAIC	BestModel Open	BestModel Close	Pc	%Confidence	95% Open	95% Close		
Intercept									
Mean	-122.092	79	79	5.00E-03	1	79	78		
Max	-122.092	79	79	5.00E-03	1	79.5	78.5		
<b>Min</b>	<b>-122.092</b>	<b>79</b>	<b>79</b>	<b>5.00E-03</b>	<b>1</b>	<b>79</b>	<b>78.5</b>		
QuadMean	-120.438	79	79	8.00E-03	1	79	78		
QuadMax	-121.959	79	78	5.00E-03	1	79.5	78		
QuadMin	-120.438	79	79	7.00E-03	1	79	78.5		
Slope									
Mean	-65.2128	81	70	6.00E-03	4	82	67		
Max	-63.1041	80	78	6.00E-03	3	77	59		
Min	-67.4966	78	68	6.00E-03	3	78	62		
QuadMean	-65.2639	81	71	8.00E-03	3	82	68		
<b>QuadMax</b>	<b>-65.9458</b>	<b>73</b>	<b>59</b>	<b>7.00E-03</b>	<b>2</b>	<b>76.5</b>	<b>58</b>		
QuadMin	-66.2425	78	68	0.009	3	78	65		

**Appendix B-II Table B8:** Overall environmental model for murre growth when sea-surface temperature is included as a predictor variable for murre growth. The prefix *slope* is used for the slope, and *Intercept* for intercept. Standard error and 95% highest posterior density intervals are shown. Non-intercept terms with 95% confidence intervals that did not overlap zero are bolded. For the fixed effects of each window the same prefixes above are used with a term after an underscore that indicates which parameter the window was identified for in the sliding window analysis. Each fixed effect has a suffix after WIN that indicates whether the window is a predicted effect of sea-surface temperature (SST). The effect of a quadratic term is indicated by E2.

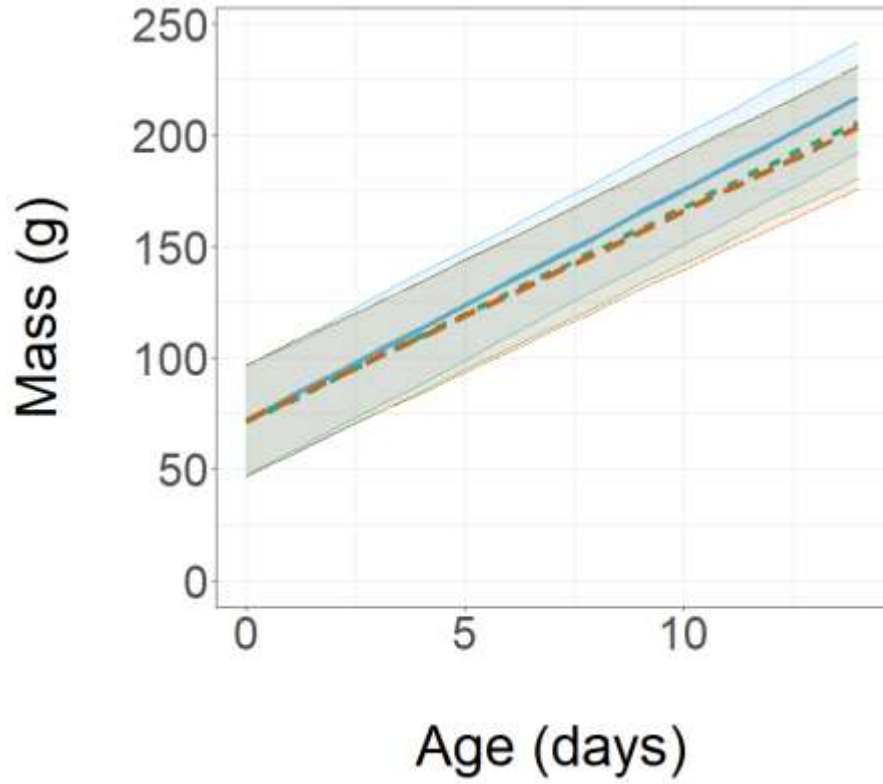
<b>Final SST Model</b> (Number of observations 6769)								
Group-Level	Effects:							
~Band.No	(Number	of	levels:	1526)				
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	
sd(Intercept)	14.64	0.35	13.96	15.32	1	2600	4960	
sd(Age)	1.83	0.06	1.71	1.96	1	3386	6317	
cor(Intercept, Age)	0.79	0.02	0.75	0.84	1	3208	5226	
~Year	(Number	of	levels:	27)				
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	
sd(Intercept)	10.37	1.7	7.62	14.33	1	2075	3936	
sd(Age)	0.73	0.14	0.49	1.05	1	2987	5094	
cor(Intercept, Age)	0.07	0.22	-0.37	0.49	1	3582	5537	
Population-Level	Effects:							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	
Intercept	128.04	14.63	98.97	156.11	1	2233	4186	
Age	7.69	1.68	4.41	10.96	1	2998	4541	
IntWinSST	1.25	4.38	-7.31	9.93	1	2183	3847	
IIntWinSSTE2	0.05	0.32	-0.6	0.68	1	2227	3915	
<b>SlopeWinSST</b>	<b>-7.24</b>	<b>2.96</b>	<b>-13.04</b>	<b>-1.35</b>	1	2251	4211	
ISlopeWinSSTE2	4.53	2.33	-0.06	9.1	1	2252	3888	
<b>Age:SlopeWinSST</b>	<b>-0.85</b>	<b>0.43</b>	<b>-1.68</b>	<b>-0.01</b>	1	3039	5287	
Age:ISlopeWinSSTE2	0.44	0.32	-0.19	1.07	1	2954	5078	
Age:IntWinSST	0.51	0.5	-0.47	1.49	1	2999	4609	
Age:IIntWinSSTE2	-0.03	0.04	-0.1	0.04	1	3085	4695	
Family	Specific	Parameters:						
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	
sigma	12.32	0.14	12.05	12.6	1	4535	6655	



**Appendix B-II Figure B1:** Windows identified in our sliding window analysis as the best predictors of either the intercept or slope of murre growth. Each bar indicates the median start and end of the top 95% models for a given variable (sea-surface temperature, air temperature, or percentage ice-cover). The top 95% of models are those that when their Akaike weights are summed together encompass 95% of the sum of all Akaike weights for models evaluated in our sliding window analysis (Bailey & Pol, 2016; van de Pol et al., 2016). For each data subset and weather variable the upper teal bar indicates the median start and end of windows that best predicts the intercept of murre growth and the purple bar below indicates the start and end of a window that predicts the slope of murre growth. Bolded bars were retained in our model selection process and faded bars were not.



**Appendix B-II Figure B2:** Model predicted effects of A) sea-surface temperature during prelaying, and scatter plots of individual growth slopes (g/day) across B) sea-surface temperature during prelaying. Individual estimates in graphs on the right (B) are the summed annual and individual group effect estimated in our baseline linear mixed effect model and they do not account for estimate error (see Hadfield et al., 2010; Houslay & Wilson, 2017), therefore the plotted relationships are just for visualization of effects identified in our sliding window analysis.



**Appendix B-II Figure B3:** Predicted growth of thick-billed murre nestlings, under average conditions across the study (blue solid line), a low emission climate change scenario (RCP2.6; green short dashed lined), and a high emission climate change scenario (RCP8.5; orange long dashed line).

## **APPENDIX B-III: MISSING DATA, CLIMWIN MODEL SELECTION & MODEL PRIORS**

### **Extraction of growth estimates and temporal changes in growth**

We estimate the individual deviation from the population mean for the growth parameters by summing the random effect estimate for a given individual chick ( $I$ ) and its hatch-year ( $Y$ ; e.g., Aldredge, 2016).

We use each individual's extracted random effect prediction as a response variable in our relative sliding window analysis. Few studies have tried to find environmental predictors of individual-level growth parameters, and a challenge exists in carrying forward error in the estimates. We acknowledge that we do not carry forward error in our analysis but running our analysis on the entire posterior distribution of an estimate would be computationally prohibitively time-consuming and expensive. To understand how our chosen growth parameters have changed over time in each study system we used linear (murre) or non-linear (gulls & kittiwakes) models of growth with a continuous mean centred linear and quadratic fixed effect of year.

### **Climwin model selection**

We based our model selection on three indicators of model explanatory power from the 'climwin' sliding window analysis (van de Pol et al., 2016): the difference between the Akaike Information Criterion of a given model and that of a model with an intercept only ( $\Delta AIC$ ); the probability of detecting the best windows as a signal just by chance ( $P_C$ ); and the extent to which several windows have similar explanatory power as the top model ( $\%CI$ ). To calculate  $P_C$ , we ran five simulation models using different randomizations of the mean phenotype across years. The  $\%CI$  is the percentage of all tested models required to reach 95% of the sum of all Akaike weights. In our model selection process, we first chose models that had the smallest  $\Delta AIC$ . We considered models with a  $\Delta AIC$  of  $<2$  to provide equal statistical support (Burnham & Anderson, 1998). Of the top models with the lowest  $\Delta AIC$ , we then chose the models with the lowest confidence set ( $\%CI$ ) and the smallest probability of being observed by chance ( $P_C$ ). If the lowest confidence set and smallest probability disagreed, we chose the model with the lowest

confidence set. We used the lowest confidence set because our models often had similarly low probabilities of being observed by chance ( $P_C$ ) but differed in their explanatory power ( $\%CI$ ).

### **Missing Climate Data**

Average sea-surface temperature around the colony was not missing for any date for any of the three species. On Middleton ~0.73% of all days were missing air temperature data, mainly in early June of 2007 and early July of 2017. Approximately 4% of the dates were missing air temperature data at the Coral Harbour weather station and the majority (~67%) of these occurred in 2015. Approximately 13% of days were missing ice-cover data for the murre dataset, of which ~58% occurred after 2011 and ~72% occurred in August. Missing data in the ice-cover dataset is caused by non-detectable amounts of ice-cover in the region, and were replaced by low ice-cover values (average of 4% ice-cover in August). Removing instead of replacing these missing data would potentially remove data on murre chicks growing in low ice-cover environments, potentially biasing our interpretation of the relationship between ice-cover and growth. Air temperature and ice-cover both had consecutive days of missing data so we used method 2 in the *climwin* function, which replaces missing data points with the mean climate of all records on the same data across years (van de Pol et al., 2016). Method 1 in *climwin* replaces missing data with climate data from dates two days before and after the date of the missing data. However, data was missing for more than two consecutive days, so we used the method 2 approach to missing data.

### **Priors and among individual and year correlations**

For both linear and non-linear models, we estimated the correlation among all linear (intercept, slope) or non-linear parameters (asymptote, relative maximum growth rate, and timing of maximum growth) at the individual and annual levels within the model. For models of non-linear growth, we estimated the shape parameter ( $d$ ) at the population level only. To aid convergence, we estimated the asymptote parameter as two orders of magnitude lower and the growth rate parameter as two orders of magnitude higher by multiplying or dividing (respectively) the parameter within the unified Richards curve by 100. We used custom normal priors for all parameters in the non-linear models and improper uniform priors for the linear model (see electronic Appendix B-III supporting information, Table S2-1).

We used the default half-student-t distribution priors with a mean of 0, and 3 degrees of freedom, and a standard deviation equal to the standard deviation of the response variable ( $W$ ; chick weight) for estimates of the individual and annual standard deviation.

**Appendix B-III Table B1:** Priors and models used for each seabird species.

Species	Model	Population Level Parameter Priors
Thick-billed Murre	Linear mixed effect model	Intercept ~ Uniform (0, 500) Slope ~ Uniform (0, 500)
Black-legged Kittiwake	Non-linear random effect Richard's model	Asymptote ~ Normal (mean = 4.0, std.dev. = 1.0) Maximum Growth ~ Normal (mean = 5.0, std.dev. = 1.0) Timing of Max. Growth ~ Normal (mean = 15.0, std.dev. = 2.0)
Glaucous-winged Gull	Non-linear random effect Richard's model	Asymptote ~ Normal (mean = 9.0, std.dev. = 1.0) Maximum Growth ~ Normal (mean = 5.0, std.dev. = 1.0) Timing of Max. Growth ~ Normal (mean = 15.0, std.dev. = 2.0)

## Appendix C: Supplementary Material for Chapter 5

### Fitness Functions

As noted in the main text we contrasted five different fitness function shapes at each survival stage. Following de Villemereuil *et al.*, (2020) we used a logit link function for our flat, linear, and planar fitness functions (eqs. 1a, 1b, & 1c) but used an exponential for the Gaussian or bivariate Gaussian fitness peak and a logit link for the  $W_{max}$  (maximum fitness) parameter (eqs 1d & 1e). In each of the below equations the survival probability is modelled as a function of either one trait (mass or wing length;  $z$ ), or two traits (mass & wing length;  $z_1$  &  $z_2$ ). The below equations correspond to the fitness functions described in the text

$$W(z) = \text{logit}(a) \quad 1a$$

$$W(z) = \text{logit}(a + bz) \quad 1b$$

$$W(z_1, z_2) = \text{logit}(a + b_1z_1 + b_2z_2) \quad 1c$$

$$W(z) = \text{logit}(W_{max}) \exp\left(-\frac{(z - \theta)^2}{2\omega^2}\right) \quad 1d$$

$$W(z_1, z_2) = \text{logit}(W_{max}) \exp\left[-\frac{\left(\frac{z_1 - \theta_1}{\omega_1^2} - \frac{2\rho(z_1 - \theta_1)(z_2 - \theta_2)}{\omega_1\omega_2} + \frac{z_2 - \theta_2}{\omega_2^2}\right)}{2(1 - \rho^2)}\right] \quad 1e$$

where  $a$  is the intercept (Eq. 1a, b, c),  $b$  is the selection differential (Eq. 1b) or gradient (Eq. 1c),  $W_{max}$  is the maximum fitness,  $\theta$  is the optimal mass or wing length (Eqs. 1d, e),  $\omega$  is the width of the fitness function (Eqs. 1d, e), and  $\rho$  is the correlation between mass and wing length (Eq. 1e).

**Appendix C Table C1:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 0 to age 5 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Bivariate Gaussian</b>	<b>0</b>
Survival from 0 to 5 Days	<b>Fluctuating Bivariate Gaussian by Group</b>	<b>1.8</b>
	Bivariate Gaussian	151.3
	Univariate Gaussian mass	160.1
	Directional mass	165.8
	Plane mass & wing	169.3
	Univariate Gaussian wing	337.7
	Directional wing	343.9
	Flat	355.3

**Appendix C Table C2:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 5 to age 10 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Linear Mass by Group</b>	<b>0</b>
	<b>Fluctuating Linear Mass</b>	<b>2.3</b>
	<b>Fluctuating Plane mass &amp; Wing by Group</b>	<b>4.7</b>
Survival from 5 to 10 Days	<b>Fluctuating Plane mass &amp; Wing</b>	<b>4.9</b>
	Directional mass	63.4
	Plane mass & wing	66.2
	Bivariate Gaussian	111.4
	Univariate Gaussian weight	144.7
	Univariate Gaussian wing	397.5
	Directional wing	360.9
	Flat	633.3

**Appendix C Table C3:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 10 to age 15 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded.

Survival Period	Model	$\Delta$ LOOIC
Survival from 10 to 15 Days	<b>Fluctuating Bivariate Plane</b>	<b>0</b>
	<b>Fluctuating Linear Mass by Group</b>	<b>1.3</b>
	<b>Fluctuating Linear Mass</b>	<b>2.3</b>
	<b>Plane mass &amp; wing</b>	<b>3.9</b>
	<b>Fluctuating Bivariate Plane by Group</b>	<b>4.2</b>
	Linear mass	9.9
	Bivariate Gaussian	56.1
	Univariate Gaussian weight	83.4
	Directional wing	143.9
	Univariate Gaussian wing	179.2
Flat	312.3	

**Appendix C Table C4:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 15 to age 20 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Bivariate Plane</b>	<b>0</b>
	<b>Fluctuating Bivariate Plane by Group</b>	<b>3.5</b>
	Plane mass & wing	18.1
	Linear mass	25
Survival from 15 to 20 Days	Bivariate Gaussian	63.4
	Univariate Gaussian weight	100.2
	Directional wing	150.2
	Univariate Gaussian wing	183.9
	Flat	329.9

**Appendix C Table C5:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 20 to age 25 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Linear Mass</b>	<b>0</b>
	<b>Linear mass</b>	<b>1.9</b>
	<b>Fluctuating Bivariate Plane</b>	<b>3.6</b>
	<b>Fluctuating Linear Mass by Group</b>	<b>3.6</b>
	<b>Plane mass &amp; wing</b>	<b>4</b>
	Bivariate Gaussian	11.4
Survival from 20 to 25 Days	Fluctuating Bivariate Plane by Group	13.4
	Univariate Gaussian weight	25.3
	Directional wing	60.6
	Univariate Gaussian wing	70.7
	Flat	148.6

**Appendix C Table C6:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 25 to age 30 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Linear Mass by Group</b>	<b>0</b>
	Fluctuating Linear Mass	5.5
	Linear mass	8.1
	Fluctuating Bivariate Plane	8.3
Survival from 25 to 30 Days	Bivariate Plane	12.3
	Bivariate Gaussian	12.8
	Univariate Gaussian weight	26.7
	Directional wing	50.9
	Univariate Gaussian wing	61.5
	Flat	87.3

**Appendix C Table C7:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 30 to age 35 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Linear Mass</b>	<b>0.0</b>
	<b>Bivariate Gaussian</b>	<b>2.7</b>
	Fluctuating Bivariate Plane	7.2
	Bivariate Plane	8
Survival from 30 to 35 Days	Fluctuating Linear Mass by Group	9
	Univariate Gaussian weight	14.5
	Fluctuating Bivariate Plane by Group	21
	Univariate Gaussian wing	36.6
	Directional wing	51.4
	Flat	69.2

**Appendix C Table C8:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 35 to age 40 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded.

Survival Period	Model	$\Delta$ LOOIC
	<b>Fluctuating Linear Mass</b>	<b>0</b>
	<b>Fluctuating Linear Mass by Group</b>	<b>1</b>
	<b>Fluctuating Bivariate Plane</b>	<b>1.7</b>
	<b>Fluctuating Bivariate Plane by Group</b>	<b>2.6</b>
Survival from 35 to 40 Days	Univariate Gaussian weight	5.1
	Linear mass	6.4
	Bivariate Plane	8
	Bivariate Gaussian	7.2
	Univariate Gaussian wing	13.3
	Flat	20.3
	Directional wing	21

**Appendix C Table C9:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 40 to fledging as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded.

Survival Period	Model	$\Delta$ LOOIC
Survival from 40 days to fledge	<b>Fluctuating Linear Mass by Group</b>	<b>0</b>
	<b>Fluctuating Linear Mass</b>	<b>0.4</b>
	Fluctuating Bivariate Plane	5.1
	Bivariate Gaussian	8.9
	Univariate Gaussian weight	9.3
	Flat	9.4
	Univariate Gaussian wing	10.8
	Directional wing	13.9
	Linear mass	17.5
Bivariate Plane	22.3	

**Appendix C Table C10:** Top fitness function for survival from age 0 to age 5 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the maximum fitness Wmax, the trait specific optimum  $\theta$ , the correlation between wing length and mass  $\rho$ , and the width of the fitness function for each trait  $\omega$ . The suffices indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the optimal mass for a non-food supplemented first-hatched nestling would be sum of  $\theta_{Mass\_First-hatched\_Fed}$  and  $\theta_{Mass\_Treatmentunfed}$ . If there is no suffix for a parameter the same parameter was assumed for all food treatment and rank groupings.

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**Age 0 Model of Selection**

**Bivariate Gaussian Synchronous Fluctuations, Total observations = 4959**

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Group-Level Effects:

Year	(Number of levels: 24)						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(Wmax)	0.64	0.43	0.04	1.64	1	1173	1347
sd( $\theta_{Mass}$ )	0.47	0.18	0.12	0.84	1.01	503	470
sd( $\theta_{Wing}$ )	3.11	0.8	1.82	4.92	1	1668	1989
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
Wmax	4.08	0.38	3.43	4.95	1	2956	1860
$\rho_{First-hatched\_Fed}$	0.14	0.2	-0.28	0.51	1	1388	1526
$\rho_{Second-hatched}$	-0.08	0.28	-0.65	0.44	1	1578	1832
$\rho_{Treatmentunfed}$	-0.37	0.24	-0.84	0.1	1	1497	1384
$\rho_{Second-hatched:Treatmentunfed}$	-0.42	0.31	-0.94	0.25	1	1405	1748
$\theta_{Mass\_First-hatched\_Fed}$	1.47	0.32	0.9	2.15	1	1514	1332
$\theta_{Mass\_Second-hatched}$	1.17	0.37	0.36	1.85	1	1599	1323
$\theta_{Mass\_Treatmentunfed}$	-0.02	0.36	-0.77	0.64	1	1301	1697
$\theta_{Mass\_Second-hatched:Treatmentunfed}$	-3.49	0.83	-5.04	-1.86	1	2325	2195
$\theta_{Wing\_First-hatched\_Fed}$	0.16	1.6	-2.95	3.36	1	1185	1505
$\theta_{Wing\_Second-hatched}$	3.15	2.88	-2.88	8.67	1	1433	1731
$\theta_{Wing\_Treatmentunfed}$	3.04	1.71	-0.12	6.78	1	1488	1882
$\theta_{Wing\_Second-hatched:Treatmentunfed}$	5.97	3.28	0.24	13.01	1	1478	1800
$\omega_{Mass}$	5.08	0.51	4.23	6.2	1	1481	1602
$\omega_{Wing}$	18.4	3.2	12.88	25.37	1	2427	2036

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**Appendix C Table C11:** Top fitness function for survival from age 5 to age 10 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicator of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior (see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings.

**Age 5 Model of Selection**

**Fluctuating Linear Mass by Group, Total observations = 4093**

Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a_{First-hatched\_Fed}$ )	0.25	0.16	0.01	0.61	1	1293	1755
sd( $a_{Second-hatched}$ )	0.52	0.21	0.11	0.95	1	1050	988
sd( $a_{Treatmentunfed}$ )	0.42	0.21	0.04	0.85	1	1019	892
sd( $a_{Second-hatched:Treatmentunfed}$ )	0.25	0.19	0.01	0.72	1	1925	1860
sd( $b_{First-hatched\_Fed}$ )	0.21	0.15	0.01	0.55	1	1219	1647
sd( $b_{Second-hatched}$ )	0.26	0.19	0.01	0.69	1	1443	1858
sd( $b_{Treatmentunfed}$ )	0.26	0.18	0.01	0.66	1	1006	1782
sd( $b_{Second-hatched:Treatmentunfed}$ )	0.35	0.26	0.01	0.97	1	1176	1419
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
$a_{First-hatched\_Fed}$	3.75	0.22	3.35	4.22	1	2689	2078
$a_{Second-hatched}$	-0.92	0.29	-1.49	-0.34	1	2233	2500
$a_{Treatmentunfed}$	-0.08	0.27	-0.64	0.46	1	2136	2316
$a_{Second-hatched:Treatmentunfed}$	-1.08	0.33	-1.72	-0.42	1	2329	2221
$b_{First-hatched\_Fed}$	1.43	0.17	1.08	1.76	1	2114	1935
$b_{Second-hatched}$	-0.09	0.23	-0.55	0.35	1	2633	2467
$b_{Treatmentunfed}$	0.11	0.21	-0.31	0.52	1	2457	2446
$b_{Second-hatched:Treatmentunfed}$	-0.22	0.28	-0.75	0.34	1	3064	2467

**Appendix C Table C12:** Top fitness function for survival from age 10 to age 15 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection gradient *b*. “\_Mass” or “\_Wing” following the parameter indicate the estimate for mass or wing length, respectively. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of *b\_First-hatched\_Fed* and *b\_Treatmentunfed*. If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings.

**Age 10 Model of Selection**

**Synchronous Fluctuating Bivariate Wing & Mass, Total observations = 3577**

Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.39	0.2	0.02	0.82	1	560	553
sd( <i>b</i> _Wing)	0.11	0.08	0.01	0.31	1	638	591
sd( <i>b</i> _Mass)	0.18	0.12	0.01	0.45	1.01	393	586
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
<i>a</i> _First-hatched_Fed	4.46	0.28	3.94	5.02	1.01	582	520
<i>a</i> _ Second-hatched	0.09	0.41	-0.66	0.88	1	609	468
<i>a</i> _Treatmentunfed	-0.5	0.32	-1.13	0.1	1	632	484
<i>a</i> _ Second-hatched:Treatmentunfed	-0.17	0.48	-1.07	0.75	1	679	618
<i>b</i> _Wing_First-hatched_Fed	-0.24	0.37	-0.96	0.55	1	589	588
<i>b</i> _Wing_ Second-hatched	-0.62	0.48	-1.58	0.27	1	667	546
<i>b</i> _Wing_Treatmentunfed	0.04	0.38	-0.71	0.78	1	674	545
<i>b</i> _Wing_ Second-hatched:Treatmentunfed	0.03	0.51	-0.9	1.05	1	708	540
<i>b</i> _Mass_First-hatched_Fed	1.32	0.33	0.68	1.94	1	562	590
<i>b</i> _ Mass_ Second-hatched	0.52	0.42	-0.27	1.32	1	622	590
<i>b</i> _ Mass_Treatmentunfed	0.09	0.35	-0.59	0.75	1	607	445
<i>b</i> _ Mass_ Second-hatched:Treatmentunfed	0.6	0.47	-0.3	1.58	1	678	627

**Appendix C Table C13:** Top fitness function for survival from age 15 to age 20 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection gradient  $b$ . “\_Mass” or “\_Wing” following the parameter indicate the estimate for mass or wing length, respectively. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings.

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**Age 15 Model of Selection**

**Synchronous Fluctuating Bivariate Wing & Mass, Total observations = 3511**

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Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a$ )	0.43	0.23	0.03	0.92	1	666	580
sd( $b_{Wing}$ )	0.24	0.16	0.02	0.57	1	719	590
sd( $b_{Mass}$ )	0.36	0.17	0.04	0.74	1	432	529
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
$a_{First-hatched\_Fed}$	4.38	0.26	3.89	4.93	1	562	629
$a_{Second-hatched}$	0.05	0.41	-0.73	0.83	1	513	464
$a_{Treatmentunfed}$	-0.07	0.33	-0.68	0.55	1	535	589
$a_{Second-hatched:Treatmentunfed}$	0.37	0.53	-0.59	1.52	1	472	603
$b_{Wing\_First-hatched\_Fed}$	-0.12	0.3	-0.7	0.46	1	541	550
$b_{Wing\_Second-hatched}$	-0.2	0.37	-0.89	0.56	1	632	522
$b_{Wing\_Treatmentunfed}$	0.39	0.35	-0.29	1.1	1	452	570
$b_{Wing\_Second-hatched:Treatmentunfed}$	-1.06	0.49	-2.03	-0.15	1	711	632
$b_{Mass\_First-hatched\_Fed}$	0.58	0.28	0	1.13	1	648	517
$b_{Mass\_Second-hatched}$	1.09	0.38	0.36	1.82	1	529	497
$b_{Mass\_Treatmentunfed}$	0.69	0.34	0.05	1.38	1	606	560
$b_{Mass\_Second-hatched:Treatmentunfed}$	0.33	0.48	-0.62	1.22	1	659	621

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**Appendix C Table C14:** Top fitness function for survival from age 20 to age 25 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings.

**Age 20 Model of Selection**

**Synchronous Fluctuating Linear Mass, Total observations = 3336**

Group-Level		Effects:						
~Year	(Number	of	levels:	24)				
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
sd( $a$ )	0.47	0.23	0.07	0.93	1	600	633	
sd( $b$ )	0.17	0.13	0.01	0.48	1	632	626	
Population-Level		Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
$a_{First-hatched\_Fed}$	4.08	0.27	3.56	4.59	1	553	590	
$a_{Second-hatched}$	0.18	0.37	-0.53	0.97	1	616	414	
$a_{Treatmentunfed}$	0.48	0.32	-0.18	1.13	1	579	444	
$a_{Second-hatched:Treatmentunfed}$	-0.2	0.54	-1.26	0.89	1	590	586	
$b_{First-hatched\_Fed}$	0.88	0.17	0.56	1.16	1	680	617	
$b_{Second-hatched}$	-0.23	0.31	-0.83	0.38	1	638	441	
$b_{Treatmentunfed}$	0.11	0.19	-0.26	0.5	1	671	530	
$b_{Second-hatched:Treatmentunfed}$	0.78	0.37	0.1	1.55	1	651	629	

**Appendix C Table C15:** Top fitness function for survival from age 25 to age 30 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari et al., 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings.

<b>Age 25 Model of Selection</b>							
<b>Heterogenous Fluctuating Linear Mass, Total observations = 3306</b>							
Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a_{First-hatched\_Fed}$ )	0.36	0.27	0.01	0.99	1	554	631
sd( $a_{Second-hatched}$ )	0.7	0.53	0.02	1.92	1	671	494
sd( $a_{Treatmentunfed}$ )	0.4	0.3	0.02	1.09	1.01	621	504
sd( $a_{Second-hatched:Treatmentunfed}$ )	1.35	0.86	0.1	3.3	1	565	628
sd( $b_{First-hatched\_Fed}$ )	0.31	0.23	0.01	0.84	1	501	590
sd( $b_{Second-hatched}$ )	0.9	0.49	0.06	1.99	1	444	495
sd( $b_{Treatmentunfed}$ )	0.27	0.22	0.01	0.82	1	616	583
sd( $b_{Second-hatched:Treatmentunfed}$ )	1.03	0.7	0.07	2.58	1	565	535
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
$a_{First-hatched\_Fed}$	4.49	0.29	3.95	5.09	1	677	639
$a_{Second-hatched}$	0.94	0.59	-0.11	2.27	1	559	591
$a_{Treatmentunfed}$	0.44	0.37	-0.3	1.17	1	536	551
$a_{Second-hatched:Treatmentunfed}$	0.74	0.79	-0.7	2.28	1	623	506
$b_{First-hatched\_Fed}$	0.57	0.24	0.07	1.04	1	596	516
$b_{Second-hatched}$	0.17	0.44	-0.67	1.01	1	737	564
$b_{Treatmentunfed}$	0.44	0.29	-0.1	1.06	1	686	580
$b_{Second-hatched:Treatmentunfed}$	0.17	0.58	-0.9	1.35	1	742	455

**Appendix C Table C16:** Top fitness function for survival from age 30 to age 35 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings.

**Age 30 Model of Selection**

**Synchronous Fluctuating Linear Mass, Total observations = 3028**

Group-Level		Effects:						
~Year	(Number	of	levels:	24)				
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
sd( $a$ )	0.53	0.27	0.08	1.14	1	569	627	
sd( $b$ )	0.25	0.15	0.02	0.6	1	708	633	
Population-Level		Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
$a_{First-hatched\_Fed}$	4.51	0.34	3.88	5.24	1.01	516	535	
$a_{Second-hatched}$	0.3	0.49	-0.63	1.2	1	628	520	
$a_{Treatmentunfed}$	0.28	0.37	-0.39	0.98	1	647	635	
$a_{Second-hatched:Treatmentunfed}$	0.61	0.69	-0.71	2.01	1.01	632	525	
$b_{First-hatched\_Fed}$	0.56	0.24	0.11	1.02	1.01	568	488	
$b_{Second-hatched}$	-0.34	0.44	-1.16	0.52	1.01	522	444	
$b_{Treatmentunfed}$	0.48	0.27	-0.07	1.01	1.01	619	552	
$b_{Second-hatched:Treatmentunfed}$	0.86	0.51	-0.18	1.85	1	654	516	

**Appendix C Table C17:** Top fitness function for survival from age 35 to age 40 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b\_First-hatched\_Fed$  and  $b\_Treatmentunfed$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings

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**Age 35 Model of Selection**

**Synchronous Fluctuating Linear Mass, Total observations = 2855**

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Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a$ )	0.32	0.27	0.01	1	1	638	602
sd( $b$ )	0.55	0.25	0.11	1.13	1	662	572
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
$a\_First-hatched\_Fed$	4.68	0.31	4.12	5.25	1	594	568
$a\_Second-hatched$	0.76	0.55	-0.27	1.89	1.01	874	548
$a\_Treatmentunfed$	1.1	0.48	0.2	2.02	1	616	591
$a\_Second-hatched:Treatmentunfed$	-0.21	0.78	-1.72	1.28	1	582	458
$b\_First-hatched\_Fed$	0.52	0.31	-0.12	1.11	1	665	576
$b\_Second-hatched$	0.05	0.49	-0.93	0.97	1	611	574
$b\_Treatmentunfed$	0.29	0.37	-0.44	0.96	1	613	547
$b\_Second-hatched:Treatmentunfed$	-0.8	0.65	-2.12	0.47	1	586	590

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**Appendix C Table C18:** Top fitness function for survival from age 40 to age fledging based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings

**Age 40 Model of Selection**

**Heterogenous Fluctuating Linear Mass, Total observations = 1912**

Group-Level	Effects:						
~Year	(Number	of	levels:	24)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a_{First-hatched\_Fed}$ )	0.48	0.37	0.02	1.33	1	687	444
sd( $a_{Second-hatched}$ )	0.89	0.65	0.03	2.4	1	626	552
sd( $a_{Treatmentunfed}$ )	0.8	0.6	0.03	2.23	1	559	591
sd( $a_{Second-hatched:Treatmentunfed}$ )	2.02	1.44	0.1	5.4	1	574	516
sd( $b_{First-hatched\_Fed}$ )	0.72	0.33	0.1	1.38	1	592	628
sd( $b_{Second-hatched}$ )	1.02	0.63	0.08	2.34	1.01	614	543
sd( $b_{Treatmentunfed}$ )	0.53	0.4	0.02	1.49	1	707	682
sd( $b_{Second-hatched:Treatmentunfed}$ )	1.43	0.95	0.07	3.43	1	607	594
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
$a_{First-hatched\_Fed}$	4.74	0.38	4.05	5.48	1	601	579
$a_{Second-hatched}$	0.3	0.62	-0.76	1.6	1	662	586
$a_{Treatmentunfed}$	0.8	0.57	-0.26	1.98	1	494	514
$a_{Second-hatched:Treatmentunfed}$	0.54	0.84	-1.01	2.3	1	585	631
$b_{First-hatched\_Fed}$	-0.22	0.34	-0.94	0.44	1	600	534
$b_{Second-hatched}$	0.15	0.48	-0.86	1.04	1.01	580	553
$b_{Treatmentunfed}$	0.29	0.41	-0.5	1.05	1	491	583
$b_{Second-hatched:Treatmentunfed}$	-0.37	0.71	-1.72	1.03	1	590	552

**Appendix C Table C19:** Among year standard deviation in fitness function parameters by selective period. Values in brackets indicate the 95% credible intervals for each estimate. Estimates are from the best model (lowest LOOIC) for each selective period. Estimates for a linear model of fitness are displayed for age 0 for comparison to all other selective periods and an estimate of selection gradient on wing length are included if the best (lowest LOOIC) or a top ( $\Delta$ LOOIC) fitness model included wing length (Ages 0, 5, 10, 15, 20, 35).

Parameter	Age				
	0	5	10	15	20
$SD(\beta_0)$	0.57 [ 0.40, 0.81]	0.58 [ 0.37, 0.87]	0.39 [0.02, 0.82]	0.43 [0.03, 0.92]	0.47 [0.07, 0.93]
$SD(\beta_{Mass})$	0.10 [ 0, 0.26]	0.19 [0.01, 0.42]	0.11 [0.01, 0.31]	0.36 [ 0.04, 0.74]	0.17 [0.01, 0.48]
$SD(\beta_{Wing})$	0.13 [ 0.01, 0.30]	0.15 [ 0.01, 0.36] *	0.11 [ 0.01, 0.45]	0.24 [0.02, 0.57]	0.14 [ 0, 0.39] *
$SD(\theta_{Mass})$	0.47 [0.12, 0.84]	-	-	-	-
$SD(\theta_{Wing})$	3.1 [1.8, 4.9]	-	-	-	-
$SD(W_{max})$	0.64 [ 0.04, 1.6]	-	-	-	-

Parameter	Age			
	25	30	35	40
$SD(\beta_0)$	0.30 [ 0.01, 0.86]	0.53 [0.08, 1.14]	0.32 [0.01, 1.0]	0.42 [0.02, 1.04]
$SD(\beta_{Mass})$	0.41 [ 0.07, 0.81]	0.25 [ 0.02, 0.60]	0.55 [0.11, 1.0]	0.83 [0.37, 1.42]
$SD(\beta_{Wing})$	-	-	0.51 [0.03, 1.18] *	-

\* Estimate is from a top model (LOOIC <5), but this parameter is not part of the best model

**Appendix C Table C20:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 0 to age 5 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
	<b>Synchronous AirWin</b>	<b>0</b>
	<b>Heterogenous AirWin</b>	<b>1.3</b>
	Annual Fluctuations Only	15
Survival from 0 to 5 Days	Synchronous SSTWin	16.5
	Heterogenous SSTWin	17.9
	Heterogenous Lagged PDO	25.9
	Heterogenous PDO	25.9
	Synchronous Lagged PDO	28.1
	Synchronous PDO	43.9

**Appendix C Table C21:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 5 to age 10 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
Survival from 5 to 10 Days	<b>Annual Fluctuations Only</b>	<b>0</b>
	<b>Heterogenous PDO</b>	<b>0.8</b>
	<b>Synchronous AirWin</b>	<b>0.9</b>
	<b>Synchronous PDO</b>	<b>0.9</b>
	<b>Synchronous Lagged PDO</b>	<b>1.8</b>
	<b>Synchronous SSTWin</b>	<b>3.2</b>
	<b>Heterogenous AirWin</b>	<b>4.4</b>
	Heterogenous Lagged PDO	8.5
	Heterogenous SSTWin	Did not Converge

**Appendix C Table C22:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 10 to age 15 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
	<b>Synchronous AirWin</b>	<b>0</b>
	<b>Synchronous SSTWin</b>	<b>2.9</b>
Survival from 10 to 15 Days	<b>Annual Fluctuations Only</b>	<b>4.8</b>
	Synchronous Lagged PDO	6.5
	Heterogenous Lagged PDO	6.7
	Synchronous PDO	7.1
	Heterogenous AirWin	7.1
	Heterogenous PDO	16.3
	Heterogenous SSTWin	Did not Converge

**Appendix C Table C23:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 15 to age 20 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
	<b>Synchronous AirWin</b>	<b>0</b>
	Heterogenous PDO	19.5
	Annual Fluctuations Only	5.4
	Synchronous SSTWin	9.4
	Synchronous PDO	9.5
	Synchronous Lagged PDO	9.5
Survival from 15 to 20 Days	Heterogenous AirWin	9.7
	Heterogenous Lagged PDO	10.4
	Heterogenous SSTWin	Did not converge

**Appendix C Table C24:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 20 to age 25 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
Survival from 20 to 25 Days	<b>Synchronous PDO</b>	<b>0</b>
	<b>Annual Fluctuations Only</b>	<b>2.9</b>
	<b>Synchronous Lagged PDO</b>	<b>3.9</b>
	<b>Synchronous SSTWin</b>	<b>4.8</b>
	Synchronous AirWin	5.8
	Heterogenous PDO	6.2
	Heterogenous AirWin	7.7
	Heterogenous SSTWin	9.8
	Heterogenous Lagged PDO	11.5

**Appendix C Table C25:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 25 to age 30 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
Survival from 25 to 30 Days	<b>Heterogenous Lagged PDO</b>	<b>0</b>
	<b>Heterogenous AirWin</b>	<b>1.1</b>
	<b>Synchronous SSTWin</b>	<b>1.6</b>
	<b>Annual Fluctuations Only</b>	<b>2.1</b>
	<b>Synchronous PDO</b>	<b>2.9</b>
	<b>Synchronous Lagged PDO</b>	<b>4.5</b>
	<b>Synchronous AirWin</b>	<b>4.6</b>
	Heterogenous PDO	7.3
	Heterogenous SSTWin	Did not converge

**Appendix C Table C26:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 30 to age 35 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
Survival from 30 to 35 Days	<b>Synchronous SSTWin</b>	<b>0</b>
	<b>Synchronous PDO</b>	<b>0.5</b>
	<b>Annual Fluctuations Only</b>	<b>1</b>
	<b>Synchronous AirWin</b>	<b>1.3</b>
	<b>Heterogenous Lagged PDO</b>	<b>2</b>
	<b>Synchronous Lagged PDO</b>	<b>2.2</b>
	<b>Heterogenous PDO</b>	<b>4.3</b>
	Heterogenous AirWin	5.6
	Heterogenous SSTWin	6.6

**Appendix C Table C27:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 35 to age 40 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC  $<5$  are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
Survival from 35 to 40 Days	<b>Annual Fluctuations Only</b>	<b>0</b>
	<b>Synchronous AirWin</b>	<b>0.9</b>
	<b>Synchronous SSTWin</b>	<b>1.3</b>
	<b>Heterogenous Lagged PDO</b>	<b>1.8</b>
	<b>Synchronous Lagged PDO</b>	<b>2.3</b>
	<b>Synchronous PDO</b>	<b>3.2</b>
	<b>Heterogenous PDO</b>	<b>3.5</b>
	Heterogenous AirWin	5.1
	Heterogenous SSTWin	Did not converge

**Appendix C Table C28:**  $\Delta$ LOOIC values for fitness functions evaluated for survival from age 0 to age 5 as a function of mass and/or wing length.  $\Delta$ LOOIC values are the differences between LOOIC values of the best model (lowest LOOIC value) and LOOIC value for a given model. Models with a  $\Delta$ LOOIC <5 are bolded. Airwin, SSTWin, PDO, and lagged PDO correspond to models with air temperature, sea-surface temperature, Pacific Decadal Oscillation, and Pacific Decadal Oscillation two years prior as predictors of fitness function parameters. Synchronous indicates a model where the environmental variable effects selection on all nestling rank and food treatment group the same way and heterogenous indicates the effects of the environmental variable effects selection differently depending on the nestling rank and food treatment.

Survival Period	Model	$\Delta$ LOOIC
	<b>Heterogenous PDO</b>	<b>0</b>
Survival from 40 to	<b>Heterogenous Lagged PDO</b>	<b>0.5</b>
Fledge	<b>Annual Fluctuations Only</b>	<b>1.1</b>
	<b>Synchronous Lagged PDO</b>	<b>2.5</b>
	<b>Synchronous AirWin</b>	<b>2.9</b>
	<b>Synchronous SSTWin</b>	<b>3.1</b>
	<b>Synchronous PDO</b>	<b>3.4</b>
	<b>Heterogenous AirWin</b>	<b>3.9</b>
	Heterogenous SSTWin	Did not converge

**Appendix C Table C29:** Top fitness function for survival from age 0 to age 5 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the maximum fitness Wmax, the trait specific optimum  $\theta$ , the correlation between wing length and mass  $\rho$ , and the width of the fitness function for each trait  $\omega$ . The suffices indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the optimal mass for a non-food supplemented first-hatched nestling would be sum of  $\theta_{Mass\_First-hatched\_Fed}$  and  $\theta_{Mass\_Treatmentunfed}$ . If there is no suffix for a parameter the same parameter was assumed for all food treatment and rank groupings. An “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

<b>Age 0 Air Temp Synchronous</b>							
Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(Wmax)	0.68	0.5	0.03	1.85	1	4495	6236
sd( $\theta_{Mass}$ )	0.46	0.19	0.11	0.87	1	2566	3388
sd( $\theta_{Wing}$ )	3.6	1.05	1.89	5.96	1	3971	5176
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
Wmax	4.35	0.42	3.62	5.25	1	9749	8081
$\rho$	0.01	0.15	-0.29	0.3	1	6216	7630
$\theta_{Mass\_First-hatched\_Fed}$	0.8	0.32	0.14	1.42	1	6281	7227
$\theta_{AirWin}$	0.14	0.06	0.04	0.27	1	5177	5841
$\theta_{Second-hatched}$	1.43	0.3	0.88	2.05	1	8631	8632
$\theta_{Treatmentunfed}$	0.3	0.29	-0.23	0.89	1	5812	7086
$\theta_{Second-hatched:Treatmentunfed}$	0.07	0.61	-1.17	1.23	1	5234	6043
$\theta_{Wing\_First-hatched\_Fed}$	4.55	1.6	1.83	8.16	1	5051	5399
$\theta_{Wing\_AirWin}$	-0.93	0.32	-1.63	-0.41	1	4911	6089
$\theta_{Wing\_Second-hatched}$	-1.48	1.76	-5.1	1.92	1	7841	8027
$\theta_{Wing\_Treatmentunfed}$	-3.48	1.19	-6.09	-1.39	1	6922	6659
$\theta_{Wing\_Second-hatched:Treatmentunfed}$	-6.82	2.74	-12.73	-2	1	6237	6369
$\omega_{Mass}$	5.04	0.47	4.23	6.07	1	8896	7224
$\omega_{Wing}$	16.48	3.31	10.98	23.89	1	4794	6169

**Appendix C Table C30:** Top fitness function for survival from age 5 to age 10 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection differential *b*. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of *b\_First-hatched\_Fed* and *b\_Treatmentunfed*. If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 5**

**Annual Variation Only**

Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.6	0.14	0.38	0.91	1	4548	7005
sd( <i>b</i> )	0.19	0.12	0.01	0.44	1	2636	3715
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<i>a</i> _First-hatched_Fed	3.75	0.25	3.28	4.24	1	4819	7537
<i>a</i> _Second-hatched	-1.06	0.27	-1.6	-0.53	1	5479	7631
<i>a</i> _Treatmentunfed	-0.27	0.25	-0.77	0.22	1	5482	7285
<i>a</i> _Second-hatched:Treatmentunfed	-0.85	0.33	-1.48	-0.21	1	5366	7462
<i>b</i> _First-hatched_Fed	1.45	0.17	1.1	1.79	1	5720	7497
<i>b</i> _Second-hatched	-0.12	0.22	-0.55	0.33	1	5568	7545
<i>b</i> _Treatmentunfed	0	0.2	-0.4	0.4	1	5563	7434
<i>b</i> _Second-hatched:Treatmentunfed	-0.14	0.28	-0.68	0.4	1	5480	8164

**Appendix C Table C31:** Top fitness function for survival from age 10 to age 15 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection gradient *b*. “\_Mass” or “\_Wing” following the parameter indicate the estimate for mass or wing length, respectively. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection gradeintl on mass for a non-food supplemented first-hatched nestling would be sum of *b\_Mass\_First-hatched\_Fed* and *b\_Mass\_Treatmentunfed*. If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 10**

**Air Temperature Synchronous**

Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.51	0.25	0.06	1.03	1	3307	3710
sd( <i>b</i> _Wing)	0.15	0.12	0.01	0.44	1	5827	6910
sd( <i>b</i> _Mass)	0.2	0.14	0.01	0.54	1	3631	5899
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<i>a</i> _First-hatched_Fed	4.4	0.33	3.76	5.07	1	10416	8827
<i>a</i> _Second-hatched	0.1	0.43	-0.71	0.95	1	11755	9942
<i>a</i> _Treatmentunfed	-0.28	0.33	-0.93	0.37	1	12051	9722
<i>a</i> _AirWin	0.05	0.06	-0.06	0.17	1	9512	8431
<i>a</i> _Second-hatched:Treatmentunfed	-0.12	0.53	-1.14	0.91	1	11821	9876
<i>b</i> _Wing_First-hatched_Fed	-0.33	0.38	-1.07	0.44	1	7748	7884
<i>b</i> _Wing_Second-hatched	-0.53	0.48	-1.47	0.42	1	9698	8594
<i>b</i> _Wing_Treatmentunfed	0	0.38	-0.74	0.76	1	7810	7929
<i>b</i> _Wing_AirWin	0.01	0.06	-0.1	0.12	1	12519	8960
<i>b</i> _Wing_Second-hatched:Treatmentunfed	0.07	0.54	-0.98	1.13	1	9770	9156
<i>b</i> _Mass_First-hatched_Fed	1.08	0.35	0.4	1.75	1	8128	8636
<i>b</i> _Mass_Second-hatched	0.15	0.45	-0.73	1.02	1	9952	8923
<i>b</i> _Mass_Treatmentunfed	0.15	0.36	-0.55	0.84	1	8504	8116
<i>b</i> _Mass_AirWin	0.12	0.05	0.02	0.22	1	11659	8865
<i>b</i> _Mass_Second-hatched:Treatmentunfed	0.81	0.52	-0.18	1.86	1	10027	8785

**Appendix C Table C32:** Top fitness function for survival from age 15 to age 20 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection gradient *b*. “\_Mass” or “\_Wing” following the parameter indicate the estimate for mass or wing length, respectively. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection gradient on mass for a non-food supplemented first-hatched nestling would be sum of *b\_Mass\_First-hatched\_Fed* and *b\_Mass\_Treatmentunfed*. If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 15**

**Air Temperature Synchronous**

Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.44	0.27	0.03	1.05	1	3448	6276
sd( <i>b</i> )	0.27	0.17	0.01	0.65	1	3870	6156
sd( <i>b_Mass</i> )	0.36	0.19	0.03	0.76	1	3273	4671
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<i>a_First-hatched_Fed</i>	4.75	0.39	4	5.53	1	10949	9156
<i>a_Second-hatched</i>	0.22	0.43	-0.59	1.08	1	15791	10032
<i>a_Treatmentunfed</i>	0	0.34	-0.67	0.67	1	17369	10185
<i>a_AirWin</i>	-0.12	0.08	-0.29	0.05	1	9362	8230
<i>a_Second-hatched:Treatmentunfed</i>	0.62	0.62	-0.56	1.87	1	15285	9732
<i>b_Wing_First-hatched_Fed</i>	0.48	0.34	-0.19	1.15	1	9386	8963
<i>b_Wing_Second-hatched</i>	0.05	0.38	-0.7	0.81	1	11794	9674
<i>b_Treatmentunfed</i>	0.42	0.33	-0.23	1.08	1	11045	8795
<i>b_Wing_AirWin</i>	-0.19	0.07	-0.33	-0.06	1	10053	9411
<i>b_Wing_Second-hatched:Treatmentunfed</i>	-0.99	0.51	-2	0.02	1	12842	9638
<i>b_Mass_First-hatched_Fed</i>	0.33	0.31	-0.26	0.95	1	10189	9335
<i>b_Mass_Second-hatched</i>	0.95	0.42	0.12	1.77	1	11180	8974
<i>b_Mass_Treatmentunfed</i>	0.56	0.33	-0.08	1.21	1	10962	9458
<i>b_Mass_AirWin</i>	0.1	0.06	-0.02	0.21	1	8849	7504
<i>b_Mass_Second-hatched:Treatmentunfed</i>	0.44	0.51	-0.56	1.45	1	11200	9384

**Appendix C Table C33:** Top fitness function for survival from age 20 to age 25 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection gradient *b*. “\_Mass” or “\_Wing” following the parameter indicate the estimate for mass or wing length, respectively. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of *b\_First-hatched\_Fed* and *b\_Treatmentunfed*. If there is no suffix for a parameter, the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 20**

**PDO Synchronous**

Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.34	0.21	0.02	0.82	1	4444	5995
sd( <i>b</i> )	0.17	0.14	0.01	0.51	1	4623	6454
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<i>a_First-hatched_Fed</i>	4.03	0.29	3.48	4.63	1	11918	8393
<i>a_Second-hatched</i>	0.22	0.42	-0.57	1.06	1	14453	10050
<i>a_Treatmentunfed</i>	0.56	0.36	-0.12	1.27	1	12989	9603
<i>a_pdo</i>	-0.16	0.18	-0.52	0.2	1	13562	9270
<i>a_Second-hatched:Treatmentunfed</i>	-0.14	0.59	-1.28	1.06	1	14361	9810
<i>b_First-hatched_Fed</i>	1.03	0.19	0.66	1.38	1	10624	8690
<i>b_Second-hatched</i>	-0.18	0.33	-0.85	0.46	1	12871	9512
<i>b_Treatmentunfed</i>	0.05	0.23	-0.4	0.49	1	12030	8973
<i>b_pdo</i>	0.18	0.11	-0.04	0.41	1	13070	9450
<i>b_Second-hatched:Treatmentunfed</i>	0.65	0.41	-0.16	1.45	1	12821	9356

**Appendix C Table C34:** Top fitness function for survival from age 25 to age 30 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection differential *b*. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of *b\_First-hatched\_Fed* and *b\_Treatmentunfed*. If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

<b>Age 25 Lagged PDO Heterogeneous</b>							
Group-Level	Effects:						
~Year	(Number	of	levels:	22)			
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.38	0.27	0.02	1.01	1	3801	4564
sd( <i>b</i> )	0.43	0.21	0.05	0.88	1	2527	3005
Population-Level	Effects:						
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
<i>a</i> _First-hatched_Fed	4.44	0.32	3.85	5.08	1	7675	7925
<i>a</i> _Second-hatched	0.7	0.56	-0.34	1.84	1	9855	8443
<i>a</i> _Treatmentunfed	0.6	0.45	-0.25	1.51	1	8236	8252
<i>a</i> _pdo_lagged	-0.52	0.3	-1.12	0.06	1	7315	7778
<i>a</i> _Second-hatched:Treatmentunfed	1	0.79	-0.57	2.52	1	9905	9133
<i>a</i> _Second-hatched:pdo_lagged	-0.01	0.49	-0.98	0.94	1	8303	8736
<i>a</i> _Treatmentunfed:pdo_lagged	0.71	0.37	0.01	1.45	1	7731	8704
<i>a</i> _Second-hatched:Treatmentunfed:pdo_lagged	0.9	0.59	-0.25	2.07	1	7926	8010
<i>b</i> _First-hatched_Fed	0.38	0.29	-0.2	0.94	1	6613	7969
<i>b</i> _Second-hatched	0.53	0.39	-0.22	1.28	1	6367	8054
<i>b</i> _Treatmentunfed	0.68	0.34	0.02	1.35	1	6096	8085
<i>b</i> _pdolagged	0	0.28	-0.54	0.57	1	6380	8118
<i>b</i> _Second-hatched:Treatmentunfed	0.16	0.48	-0.78	1.13	1	6754	7898
<i>b</i> _Second-hatched:pdo_lagged	0.51	0.4	-0.27	1.3	1	6629	8057
<i>b</i> _Treatmentunfed:pdo_lagged	0.3	0.31	-0.32	0.88	1	6298	8058
<i>b</i> _Second-hatched:Treatmentunfed:pdo_lagged	-0.43	0.47	-1.35	0.48	1	6095	7294

**Appendix C Table C35:** Top fitness function for survival from age 30 to age 35 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 30**

**SST Synchronous**

Group-Level	Effects:							
~Year	(Number	of	levels:	22)				
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
sd( $a$ )	0.54	0.3	0.04	1.19	1	3868	4189	
sd( $b$ )	0.23	0.16	0.01	0.62	1	3773	5996	
Population-Level	Effects:							
	Estimate	Est.Error	l-95% CI	u-95%CI	Rhat	Bulk_ESS	Tail_ESS	
$a_{First-hatched\_Fed}$	0.98	0.87	-0.68	2.71	1	10638	9274	
$a_{Second-hatched}$	-0.01	0.5	-0.97	0.99	1	18865	9670	
$a_{Treatmentunfed}$	0.19	0.41	-0.62	0.97	1	16119	8248	
$a_{SSTWin}$	0.39	0.09	0.21	0.56	1	10687	9177	
$a_{Second-hatched:Treatmentunfed}$	0.84	0.68	-0.46	2.19	1	17594	9564	
$b_{First-hatched\_Fed}$	-0.77	0.7	-2.14	0.58	1	10911	9691	
$b_{Second-hatched}$	-0.37	0.46	-1.28	0.54	1	12921	9711	
$b_{Treatmentunfed}$	0.45	0.28	-0.09	1.02	1	16080	9956	
$b_{SSTWin}$	0.15	0.07	0.02	0.28	1	10834	9153	
$b_{Second-hatched:Treatmentunfed}$	0.85	0.52	-0.16	1.86	1	11923	9406	

**Appendix C Table C36:** Top fitness function for survival from age 35 to age 40 based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicate of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior(see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept *a*, and the selection differential *b*. The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of *b\_First-hatched\_Fed* and *b\_Treatmentunfed*. If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

**Age 35**

**Annual Fluctuations**

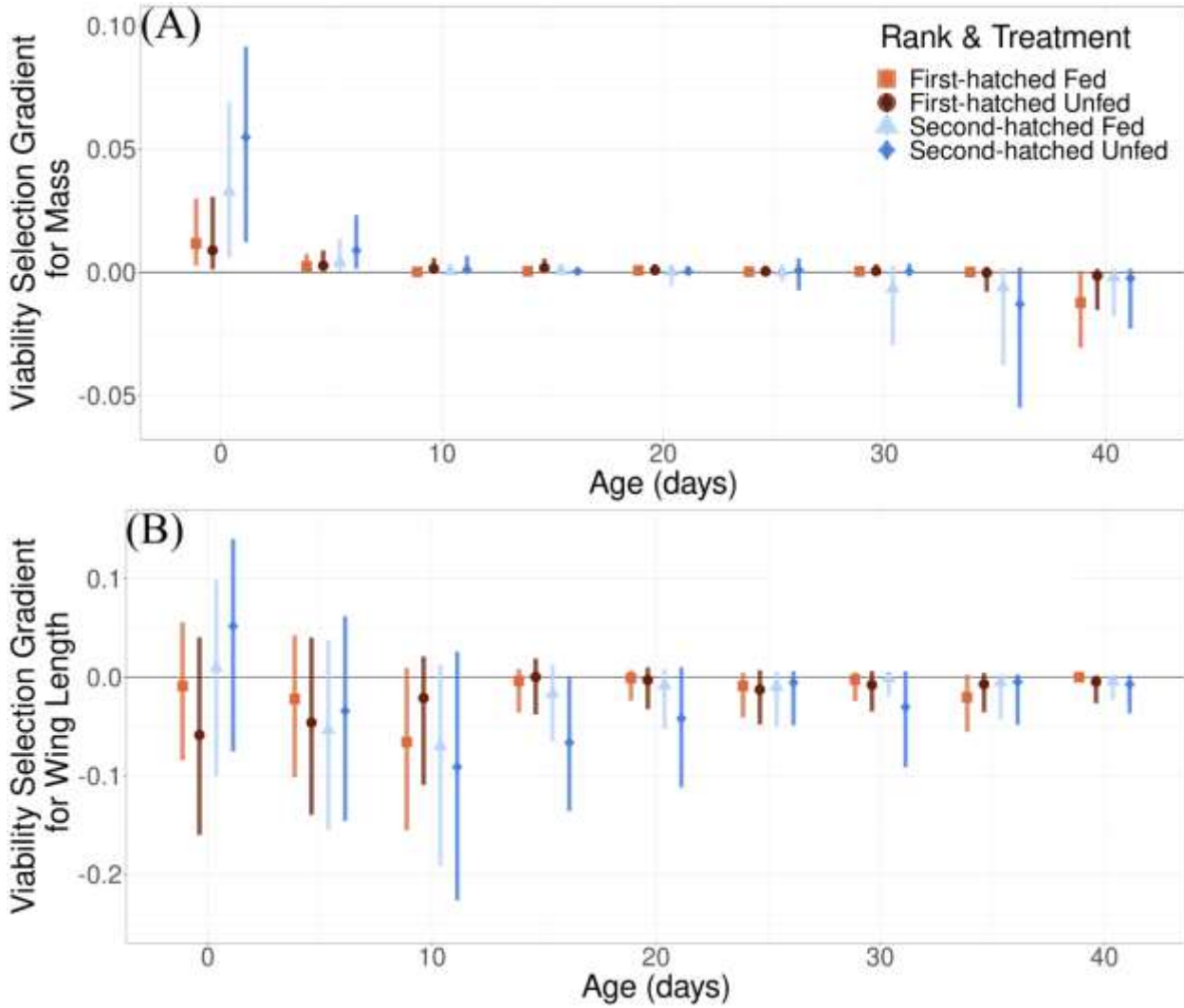
Group-Level		Effects:					
~Year	(Number of	levels:	22)				
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( <i>a</i> )	0.33	0.26	0.01	0.99	1	5487	5417
sd( <i>b</i> )	0.55	0.25	0.11	1.1	1	4149	3332
Population-Level		Effects:					
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<i>a</i> _First-hatched_Fed	4.65	0.32	4.04	5.31	1	10431	7944
<i>a</i> _Second-hatched	0.77	0.55	-0.27	1.91	1	12397	9109
<i>a</i> _Treatmentunfed	1.08	0.48	0.18	2.05	1	10986	9229
<i>a</i> _Second-hatched:Treatmentunfed	-0.2	0.78	-1.71	1.38	1	12789	8949
<i>b</i> _First-hatched_Fed	0.53	0.32	-0.1	1.14	1	8036	8314
<i>b</i> _Second-hatched	0.04	0.48	-0.93	0.96	1	10275	9252
<i>b</i> _Treatmentunfed	0.3	0.37	-0.43	1.02	1	7826	8187
<i>b</i> _Second-hatched:Treatmentunfed	-0.85	0.66	-2.16	0.41	1	10098	8978

**Appendix C Table C37:** Top fitness function for survival from age 40 to fledging based on  $\Delta$ LOOIC comparisons. For each model parameter the mean (Estimate), standard deviation (Est. Error), lower 95% credible interval (l-95% CI), and upper 95% credible interval (u-95% CI) are reported for the posterior distribution of that parameter. Rhat is an indicator of convergence of chains and if it is considerably greater than 1 the chains have not converged. The Bulk effective sampling size (Bulk\_ESS) is a diagnostic for sampling efficiency of the bulk of the posterior and the tail effective sampling size (Tail\_ESS) is a diagnostic for sampling efficiency of the tails of the posterior (see Bürkner, 2017; Vehtari *et al.*, 2017). Parameters under the “Population-Level” heading indicate fitness function parameters estimated across the entire dataset. Parameters under the “Group Level” heading indicate variation (standard deviation) in annual mean deviations from the population level parameters. The different parameters estimated are the fitness intercept  $a$ , and the selection differential  $b$ . The suffixes indicate the treatment and nestling rank level that a parameter was estimated at relative to the first-hatched food supplemented nestling group. For example, the selection differential on mass for a non-food supplemented first-hatched nestling would be sum of  $b_{First-hatched\_Fed}$  and  $b_{Treatmentunfed}$ . If there is no suffix for a parameter the same parameter value was estimated for all food treatment and rank groupings. A “AirWin”, “SSTWin”, “pdo”, or “pdo\_lagged” suffix indicates the estimate of the linear relationship between a function parameter and our chosen air temperature, sea-surface temperature, Pacific Decadal Oscillation, or lagged Pacific Decadal Oscillation parameters.

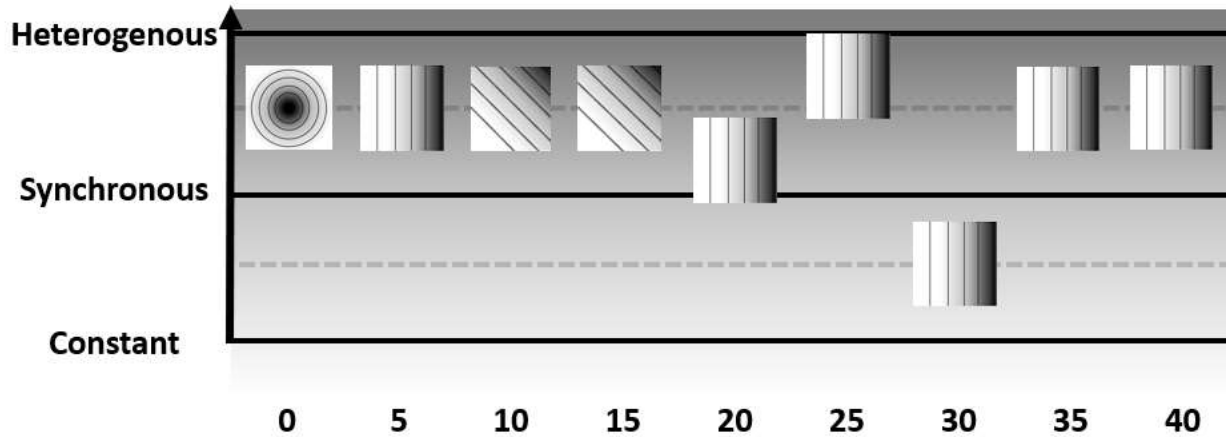
**Age 40**

**PDO Synchronous**

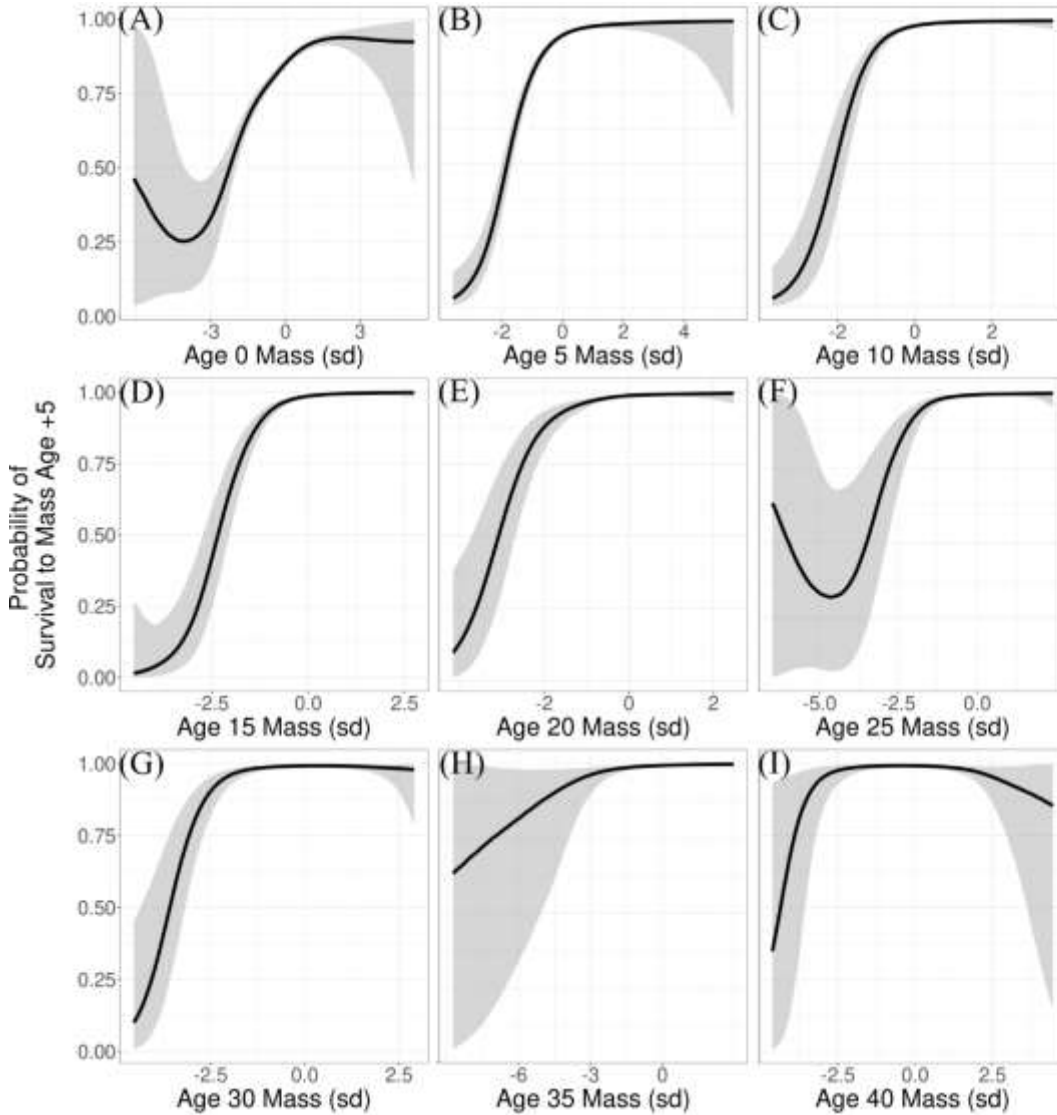
Group-Level		Effects:					
~Year	(Number of	levels:	22)				
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd( $a$ )	0.53	0.39	0.02	1.46	1	3617	6071
sd( $b$ )	0.82	0.29	0.3	1.46	1	4468	3742
Population-Level		Effects:					
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
$a_{First-hatched\_Fed}$	4.57	0.38	3.87	5.35	1	10367	8428
$a_{Second-hatched}$	-0.23	0.46	-1.12	0.68	1	12939	8996
$a_{Treatmentunfed}$	0.45	0.48	-0.46	1.42	1	13226	9714
$a_{pdo}$	-0.26	0.26	-0.8	0.22	1	8583	5808
$a_{Second-hatched:Treatmentunfed}$	0.4	0.75	-1.01	1.91	1	14249	9498
$b_{First-hatched\_Fed}$	-0.1	0.36	-0.79	0.63	1	8358	8503
$b_{Second-hatched}$	0.25	0.4	-0.52	1.04	1	11437	9723
$b_{Treatmentunfed}$	0.32	0.38	-0.42	1.08	1	10130	9353
$b_{pdo}$	0.19	0.24	-0.29	0.64	1	7826	8208
$b_{Second-hatched:Treatmentunfed}$	0.21	0.57	-0.88	1.33	1	10676	9147



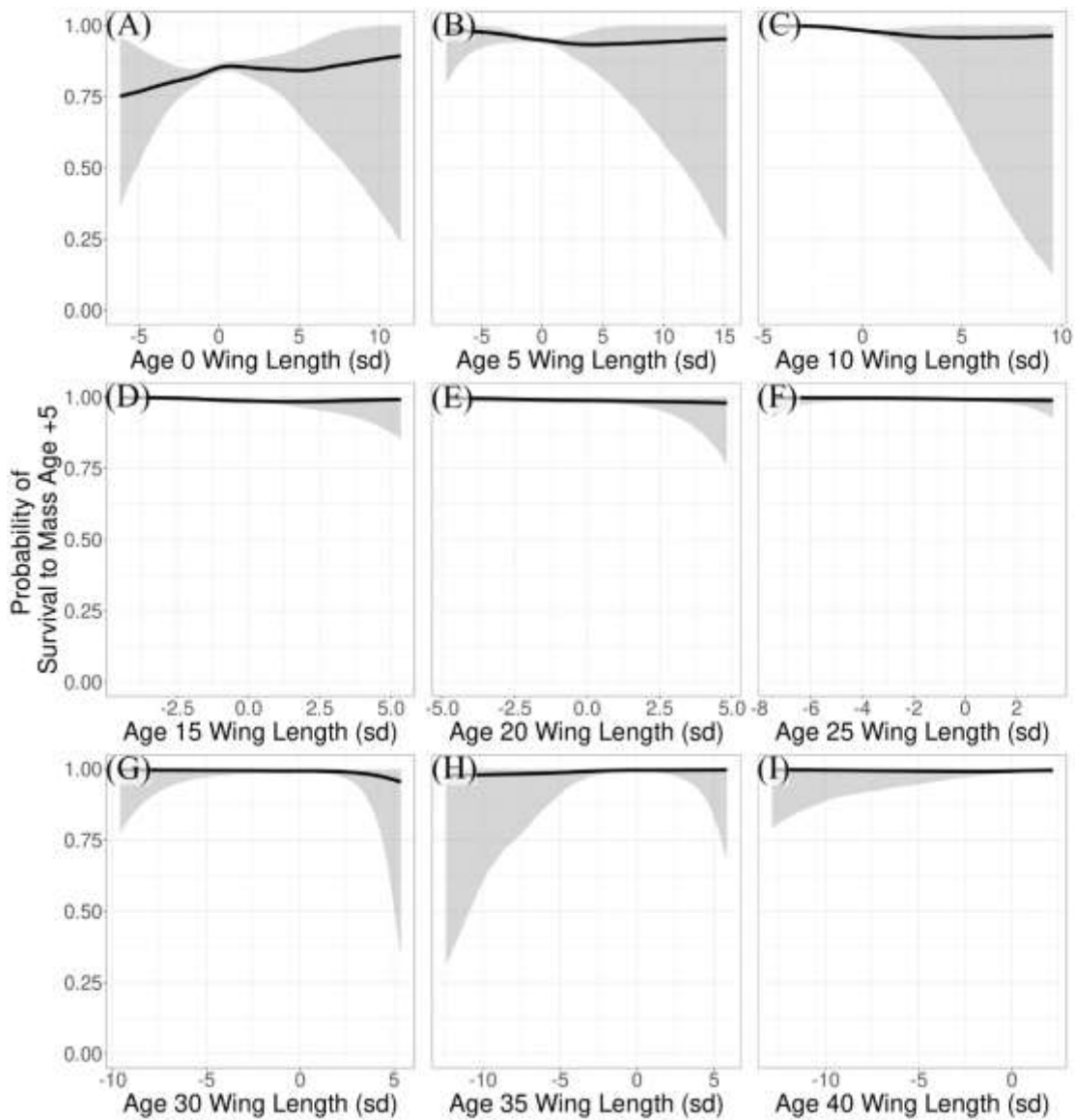
**Appendix C Figure C1:** Viability selection gradients for absolute A) mass and B) wing length. Selection gradients are transformed from logistic regression to the data scale following Janzen and Stern 1998 and Villemereuil et al. 2020. Points and 95% confidence intervals are coloured and grouped by nestling rank and food treatment groups. Brown colours indicate first hatched nestlings and blue colours indicate second hatched nestlings. Lighter colours indicate food supplemented nestlings while darker colours indicate non-food supplemented nestlings.



**Appendix C Figure C2:** Summary of selection functions and variability of selection parameters for each selective period (Age in number of days on the X-axis). On the Y-axis the “constant” indicates no annual variation in selection parameters, the “synchronous” that selection parameters varied similarly for all nestling rank and food treatment groups, and the “heterogenous” that each nestling rank and group varied differentially. For each selective period, a representative function is plotted indicating the best fitness function (based on LOOIC). Concentric circles on a square indicate a bivariate Gaussian function, diagonal lines on a square indicate a bivariate plane, and vertical lines on a plane indicate a linear function of mass. Position along the y-axis roughly corresponds to the proportion of top models that included a particular variance structure. For example, the best model for survival from age 5 to 10 was a linear model of mass and 50% of the top models included group specific fluctuations in selection.



**Appendix C Figure C3:** Generalized additive model predicted survival as a function of nestling age specific mass. Plots A, B, C, D, E, F, G, H, & I correspond to survival to age 5, 10, 15, 20, 25, 30, 35, 40, & fledging. For each age class survival functions with associated 95% credible intervals (shaded areas) are displayed.



**Appendix C Figure C4:** Generalized additive model predicted survival as a function of nestling age specific wing length. Plots A, B, C, D, E, F, G, H, & I correspond to survival to age 5, 10, 15, 20, 25, 30, 35, 40, & fledging. For each age class survival functions with associated 95% credible intervals (shaded areas) are displayed.

## Appendix C References

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