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

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Growth is a vital trait likely to be altered by climate change. We found time periods in the breeding season that correlate with growth and suggest that these effects depend on sibling interactions.

Author Contributions: DS, AC, SAH, and VLF conceived the ideas and designed methodology; SAH oversaw collection of the data; DS analysed the data; DS led the writing of the manuscript.

All authors contributed critically to the drafts, gave final approval for publication, and declare no conflict of interests.

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.

Keywords: climate change, development, early-life, phenotypic change, sibling interactions

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

66 ambient temperature (e.g. Angilletta 2009 pg.159; Vega-Trejo et al. 2018). For many animal
67 species, such inter-individual variation will be challenging to measure, but in theory, different
68 growth responses could play an important role in adaptive or maladaptive responses to novel
69 environmental conditions (Chevin et al. 2013).

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

85 We framed our hypotheses around three parameters of a nestling growth curve
86 (Supplementary File Fig. S1; Table 1): the asymptote (maximum weight), the timing of
87 maximum growth (inflection point), and the maximum relative growth rate (growth rate; Tjørve
88 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 *Anoplopoma fimbria*, salmon *Oncorhynchus* 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 first-hatched nestling shared a nest with a second-hatched nestling (Merkling et al. 2016; H3).

Materials and methods

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 *ad libitum* 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 chosen 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 were 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).

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

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.

Statistical Analyses

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; Tjørvæ and Tjørvæ 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, ε 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, 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 (ε) standard deviation. Details of a similar model we use to evaluate whether there are trends in growth parameters across years are included in Supplementary File S1.

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 the Supplementary File S1.

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.

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 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 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 Supplementary File S1. 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.

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).

Results

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 was correlated in all models (Supplementary Table S1). In more recent years unfed alpha, unfed beta, and fed beta nestlings had on average lighter asymptotes than at the beginning of the study (Supplementary File Tables S2-3, S5). However, there were no linear or quadratic trends over time for the fed alpha nestlings' asymptote (Supplementary File Tables 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. 1; Supplementary File 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 (Supplementary File Table S6, S7).

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

Average sea-surface and air temperatures varied among years (Supplementary File Tables S10, S11; Supplementary File Figs. S11, S12). The average sea-surface temperature during the breeding season increased by 0.43°C over the course of the study ($\text{CI} = [0.05^{\circ}\text{C}, 0.81^{\circ}\text{C}]$; or 0.02°C per year, $\text{CI} = [0.002^{\circ}\text{C}, 0.04^{\circ}\text{C}]$) and air temperatures during the breeding season increased by 0.74°C ($\text{CI} = [0.32^{\circ}\text{C}, 1.15^{\circ}\text{C}]$; or 0.04°C per year, $\text{CI} = [0.02^{\circ}\text{C}, 0.05^{\circ}\text{C}]$).

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 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 2; Supplementary File Table S8). We identified fewer windows from the sliding window analysis that predicted growth variation for the food-supplemented nestlings (Table 2; Supplementary File 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 (Supplementary File Figs. S3-S8).

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. 2; Supplementary File Table S12; Table 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 A, B; Table 3; Supplementary File Table S13). 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. 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 6B).

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; Supplementary File Fig. S9). None of the windows that our sliding window analysis identified impacted growth parameters in fed beta nestlings (Table 3).

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 (Supplementary File 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. 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 (Supplementary File Fig. S10 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 (Supplementary File Fig. S10 C).

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 (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 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.

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 (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).

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 (P2.2). However, our results indicated that warmer air temperatures correlated with alpha nestlings that grow to a heavier asymptote (Fig. 2; Supplementary File Table S12) yet slower-growing beta nestlings that reach a lighter asymptote (Fig. 3A, B; Supplementary File Table S13). 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 33⁰ C and 35⁰ 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 (Supplementary File 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.

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 result 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. 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. 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 in difficult warm environmental conditions might be parents that are investing extensive effort into both the alpha and beta nestlings (Weimerskirch 1992; Winkler 1987).

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 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 (Supplementary File Fig. S10 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 (Supplementary File Fig. S10 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.

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 fecundity 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 focussed 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.

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Declarations

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

Ethics Approval

Research was conducted under the approval of the USGS Alaska Science Center IACUC, in accordance with United States laws and under permits from the U.S. Fish and Wildlife Service and the State of Alaska.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The data is available from figshare. doi: 10.6084/m9.figshare.16734874

Code availability

464 The code is available from figshare. doi: 10.6084/m9.figshare.16734874

465 **References**

466 Andreasson F, Nord A, Nilsson JA (2018) Experimentally increased nest temperature affects
467 body temperature, growth and apparent survival in blue tit nestlings. *J. Avian Biol.*
468 49:e01620 doi: 10.1111/jav.01620

469 Andrew SC, Hurley LL, Mariette MM, Griffith SC (2017) Higher temperatures during
470 development reduce body size in the zebra finch in the laboratory and in the wild. *J. Evol.*
471 *Biol.* 30:2156–2164 doi: 10.1111/jeb.13181

472 Angilletta MJ (2009) Thermal adaptation: A theoretical and empirical Synthesis. Oxford
473 University Press, Oxford.

474 Bateson P (1979) How do sensitive periods arise and what are they for? *Anim. Behav.* 27:470–
475 486 doi: 10.1016/0003-3472(79)90184-2

476 Bech C, Martini S, Brent R, Rasmussen J (1984) Thermoregulation in newly hatched black-
477 legged kittiwakes. *Condor* 86:339–341 doi: 10.2307/1367006

478 Brannelly LA, Ohmer MEB, Saenz V, Richards- Zawacki CL (2019) Effects of hydroperiod on
479 growth, development, survival and immune defences in a temperate amphibian. *Funct.*
480 *Ecol.* 33:1952–1961 doi: 10.1111/1365-2435.13419

481 Braun BM, Hunt GL (1983) Brood reduction in black-legged kittiwakes. *Auk* 100:469-476 doi:
482 10.1093/auk/100.2.469

483 Bürkner PC (2017) brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat.*
484 *Softw.* 80:1–28 doi: 10.18637/jss.v080.i01

485 Chevin LM, Collins S, Lefèvre F (2013) Phenotypic plasticity and evolutionary demographic
486 responses to climate change: Taking theory out to the field. *Funct. Ecol.* 27:967–979 doi:
487 10.1111/j.1365-2435.2012.02043.x

488 Cooper EB, Kruuk LEB (2018) Ageing with a silver-spoon: A meta-analysis of the effect of
489 developmental environment on senescence. *Evol. Lett.* 2:460–471 doi: 10.1002/evl3.79

490 Cotto O, Sandell L, Chevin LM, Ronce O (2019) Maladaptive shifts in life history in a changing
491 environment. *Am. Nat.* 194:558-573 doi: 10.1086/702716

492 Coulson JC, Porter JM (1985) Reproductive success of the Kittiwake *Rissa tridactyla*: the roles
493 of clutch size, chick growth rates and parental quality. *Ibis* 127:450-466 doi:
494 10.1111/j.1474-919X.1985.tb04841.x

495 Coulson JC (2002) Why do adult kittiwakes survive so long but breed so poorly in the Pacific. *J.*
496 *Avian Biol.* 33:111-112 doi: 10.1034/J.1600-048X.2002.T01-1-330201.X

497 Cunningham SJ, Martin RO, Hojem CL, Hockey PAR (2013) Temperatures in excess of critical
498 thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a
499 study of common fiscals. *PLOS ONE* 8:e74613 doi: 10.1371/journal.pone.0074613

500 Dmitriew CM (2011) The evolution of growth trajectories: what limits growth rate? *Biol. Rev.*
501 86:97–116 doi: 10.1111/j.1469-185X.2010.00136.x

502 Drummond H (2001) A revaluation of the role of food in broodmate aggression. *Anim. Behav.*
503 61:517–526 doi: 10.1006/anbe.2000.1641

504 Emlen ST, Wrege PH, Demong NJ, Hegner RE (1991) Flexible growth rates in nestling white-
505 fronted bee-eaters: a possible adaptation to short-term food shortage. *Condor* 93:591–597
506 doi: 10.2307/1368191

English S, Fawcett TW, Higginson AD, Trimmer PC, Uller T (2016) Adaptive use of information during growth can explain long-term effects of early life experiences. *Am. Nat.* 187:620–632 doi: 10.1086/685644

Gill VA, Hatch SA (2002) Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *J. Avian Biol.* 33:113–126. doi: 10.1034/j.1600-048x.2002.330201.x

van Gils JA, Lisovski S, Lok T, Meissner W, Ozarowska A, de Fouw J, Rakhimberdiev E, Soloviev MY, Piersma T, Klaassen M (2016) Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352:819–821 doi: 10.1126/science.aad6351

Giordano M, Groothuis TGG, Tschirren B (2014) Interactions between prenatal maternal effects and posthatching conditions in a wild bird population. *Behav. Ecol.* 25:1459–1466 doi: 10.1093/beheco/aru149

Furness RW (2016) Impacts and effects of ocean warming on seabirds. In: Laffoley D, Baxter JM (eds) *Explaining Ocean Warming: Causes, Scale, Effects and Consequences* IUCN, Gland, Switzerland, pp 271-288.

Hatch SA (2013) Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Mar. Ecol. Prog. Ser.* 477:271–284 doi: 10.3354/meps10161

Hatch SA, Robertson GJ, Baird PH (2020). Black-legged Kittiwake (*Rissa tridactyla*), version 1.0. In: Billerman SM (ed) *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.bklkit.01

Hedd A, Ryder JL, Cowen LL, Bertram DF (2002) Inter-annual variation in the diet, provisioning and growth of Cassin's auklet at Triangle Island, British Columbia:

530 responses to variation in ocean climate. *Mar. Ecol. Prog. Ser.* 229:221–232 doi:
531 10.3354/meps229221

532 Hiraldo F, Veiga JP, Máñez M (1990) Growth of nestling black kites *Milvus migrans*: effects of
533 hatching order, weather and season. *J. Zool.* 222:197–214 doi: 10.1111/j.1469-
534 7998.1990.tb05672.x

535 Huchard E, Charmantier A, English S, Bateman A, Nielsen JF, Clutton-Brock T (2014) Additive
536 genetic variance and developmental plasticity in growth trajectories in a wild cooperative
537 mammal. *J. Evol. Biol.* 27:1893–1904 doi:10.1111/jeb.12440

538 Intergovernmental Panel on Climate Change (2018) Global Warming of 1.5°C. IPCC, Geneva,
539 Switzerland.

540 Kingsolver JG, Diamond SE (2011) Phenotypic selection in natural populations: what limits
541 directional selection? *Am. Nat.* 177:346–357 doi: 10.1086/658341

542 Kruuk, LEB, Osmond HL, Cockburn A (2015) Contrasting effects of climate on juvenile body
543 size in a Southern Hemisphere passerine bird. *Glob. Chang. Biol.* 21: 2929–2941 doi:
544 10.1111/gcb.12926

545 Lindström J (1999) Early development and fitness in birds and mammals. *Trends Ecol. Evol.*
546 14:343–348 doi: 10.1016/S0169-5347(99)01639-0

547 Maness TJ, Anderson DJ (2013) Predictors of juvenile survival in birds. *Ornithol. Monogr.* 78:1–
548 55 doi: 10.1525/om.2013.78.1.1

549 Marques-Stantos F, Dingemanse NJ (2020) Weather effects on nestling survival of great tits vary
550 according to the developmental stage. *J. Avian Biol.* 51:e02421 doi: 10.1111/jav.02421

551 Marshall DJ, Uller T (2007) When is a maternal effect adaptive? *Oikos* 116 :1957–1963 doi:
552 10.1111/j.2007.0030-1299.16203.x

553 McAdam AG, Boutin S (2003) Effects of food abundance on genetic and maternal variation in
 554 the growth rate of juvenile red squirrels. *J. of Evol. Biol.* 16:1249–1256 doi:
 555 10.1046/j.1420-9101.2003.00630.x

556 McKinnon L, Picotin M, Bolduc E, Juillet C, Bêty J (2012) Timing of breeding, peak food
 557 availability, and effects of mismatch on chick growth in birds nesting in the High Arctic.
 558 *Can. J. Zool.* 90:961–971 doi: 10.1139/z2012-064

559 McKinnon L, Nol E, Juillet C (2013) Arctic-nesting birds find physiological relief in the face of
 560 trophic constraints. *Sci. Rep.* 3:1816 doi: 10.1038/srep01816

561 Merkling T, Chastel O, Blanchard P, Trouvé C, Hatch SA, Danchin E (2014) Physiological and
 562 fitness correlates of experimentally altered hatching asynchrony magnitude in chicks of a
 563 wild seabird. *Gen. Comp. Endocrinol.* 198:32–38 doi: 10.1016/j.ygcen.2013.12.011

564 Merkling T, Perrot C, Helfenstein F, Ferdy JB, Gaillard L, Lefol E, Voisin E, Hatch SA, Danchin
 565 E, Blanchard P (2016) Maternal effects as drivers of sibling competition in a parent–
 566 offspring conflict context? An experimental test. *Ecol. Evol.* 6:3699–3710 doi:
 567 10.1002/ece3.1777

568 Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends*
 569 *Ecol. Evol.* 16:254–260 doi: 10.1016/S0169-5347(01)02124-3

570 Mock DW, Parker GA (1997) *The Evolution of Sibling Rivalry*. Oxford University Press,
 571 Oxford.

572 Mousseau TA, Fox CW (1998) The adaptive significance of maternal effects. *Trends Ecol. Evol.*
 573 13:403–407 doi: 10.1016/S0169-5347(98)01472-4

574 Mueller AJ, Miller KD, Bowers EK (2019) Nest microclimate during incubation affects
 575 posthatching development and parental care in wild birds. *Sci. Rep.* 9:5161 doi:
 576 10.1038/s41598-019-41690-4

577 Noble DWA, Stenhouse V, Schwanz LE (2018) Developmental temperatures and phenotypic
 578 plasticity in reptiles: a systematic review and meta-analysis. *Biol. Rev.* 93:72–97 doi:
 579 10.1111/brv.12333

580 Osborne O, O'Hara P, Whelan S, Zandbergen P, Hatch S, Elliott K (2020) Breeding seabirds
 581 increase foraging range in response to an extreme marine heatwave. *Mar. Ecol. Prog. Ser.*
 582 646:161–173 doi: 10.3354/meps13392

583 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev.*
 584 *Ecol. Evol. Syst.* 37:637–669 doi: 10.1038/nature01286

585 van de Pol M, Bailey LD, McLean N, Rijdsdijk L, Lawson CR, Brouwer L (2016) Identifying the
 586 best climatic predictors in ecology and evolution. *Methods Ecol. Evol.* 7:1246–1257 doi:
 587 10.1111/2041-210X.12590

588 Rodríguez S, Barba E (2016) Nestling growth is impaired by heat stress: an experimental study
 589 in a mediterranean great tit population. *Zool. Stud.* 55:e40 doi: 10.6620/ZS.2016.55-40

590 Rollinson N, Rowe L (2015) Persistent directional selection on body size and a resolution to the
 591 paradox of stasis. *Evol.* 69:2441–2451 doi: 10.1111/evo.12753

592 Roudybush, TE., Grau, CR, Petersen, MR, Ainley, DG, Hirsch KV, Gilman, AP, Patten SM
 593 (1979). Yolk formation in some charadriiform birds. *Condor*, 81:293–298. doi:
 594 10.2307/1367636

595 Sauve D, Friesen, VL, Charmantier, A (2021) The effects of weather on avian growth and
596 implications for adaptation to climate change. *Front. Ecol. Evol.* 9:569741. doi:
597 10.3389/fevo.2021.569741

598 Schultner J, Kitaysky AS, Gabrielsen GW, Hatch SA, Bech C (2013) Differential reproductive
599 responses to stress reveal the role of life-history strategies within a species. *Proc. Biol.*
600 *Sci.* 280:20132090 doi: 10.1098/rspb.2013.2090

601 Shizuka D, Lyon BE (2013) Family dynamics through time: brood reduction followed by
602 parental compensation with aggression and favouritism. *Ecol. Lett.* 16:315–322 doi:
603 10.1111/ele.12040

604 Sugden LG, Driver EA, Kingsley MCS (1981) Growth and energy consumption by captive
605 mallards. *Can. J. Zool.* 59:1567–1570 doi: 10.1139/z81-213

606 Suryan RM, Saba VS, Wallace BP, Hatch SA, Frederiksen M, Wanless S (2011) Environmental
607 forcing on life history strategies: Evidence for multi-trophic level responses at ocean
608 basin scales. *Prog. Oceanogr.* 81:214–222 doi: 10.1016/j.pocean.2009.04.012

609 Teplitsky C, Millien V (2014) Climate warming and Bergmann’s rule through time: is there any
610 evidence? *Evol. Appl.* 7:156–168 doi: 10.1111/eva.12129

611 Thompson SA, García- Reyes M, Sydeman WJ, Arimitsu ML, Hatch SA, Piatt JF (2019) Effects
612 of ocean climate on the length and condition of forage fish in the Gulf of Alaska. *Fish.*
613 *Oceanogr.* 28:658–671 doi: 10.1111/fog.12443

614 Tjørve KMC, Tjørve E (2017) A proposed family of Unified models for sigmoidal growth. *Ecol.*
615 *Model.* 359:117–127 doi: 10.1016/j.ecolmodel.2017.05.008

Vega-Trejo R, Head ML, Jennions MD, Kruuk LEB (2018) Maternal-by-environment but not
genotype-by-environment interactions in a fish without parental care. *Heredity* 120:154–
167 doi: 10.1038/s41437-017-0029-y

Weimerskirch H (1992) Reproductive effort in long-lived birds: age-specific patterns of
condition, reproduction and survival in the wandering albatross. *Oikos* 64:464–473 doi:
10.2307/3545162

Williams T (2012) *Physiological Adaptations for Breeding in Birds*. Oxford University Press,
Oxford.

Williams TD, Groothuis TGG (2015) Egg quality, embryonic development, and post-hatching
phenotype: an integrated perspective. In: Deeming DC, Reynolds SJ (eds), *Nests, eggs,
and incubation: New ideas about avian reproduction*. Oxford University Press, Oxford.

Winkler DW (1987) A general model for parental care. *Am. Nat.* 130:526–543 doi:
10.1086/284729

639 **Tables**640 **Table 1:** Hypotheses (H) and predictions (P) tested in the present study, with the associated

641 statistical test and result tables and figures.

	Hypothesis or prediction	Test or Result
H1	<i>Traits expressed early in growth are more influenced by environmental conditions before hatching than by conditions after hatching</i>	Sliding Window Analysis & Environmental Models of Growth
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 2; Supplementary File Table S8
P1.2	Confidence intervals of the estimated effects of environmental windows will not overlap zero in environmental models of growth.	Table 3; Supplementary File Tables S12 - S16
H2.1	<i>Warmer sea-surface temperatures result in conditions that make nestling growth poor</i>	Environmental Models of Growth
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. 2, 3 Supplementary File Tables S12 to S16
H2.2	<i>Colder air temperatures result in poor nestling growth</i>	Environmental Models of Growth
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. 2, 3; Supplementary File Tables S12 to S16
H2.3	<i>Increased food availability increases the energy budget of nestlings allowing them to maintain growth under variable environmental conditions</i>	Environmental Models of Food-Supplemented Nestlings & Interaction Terms
P2.3.1	Food-supplemented nestlings are less affected by air temperature during growth.	Supplementary File Figs. S9, 10; Supplementary File Table S14
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; Supplementary File Tables S12, S13
H3	<i>Alpha nestlings that have to compete with beta siblings expend more energy, which makes them more sensitive to environmental conditions</i>	Environmental and Sibling Overlap Models of Alpha Nestling Growth
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. 2; Supplementary File Fig. S10; Supplementary File Tables S15 & S16

Table 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 Supplementary File table S8.

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

* Indicates windows for which the effect was retained in our environmental model for the growth

of this nestling group.

Table 3: Summarized impacts of air and sea-surface temperature on nestling kittiwake growth.

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

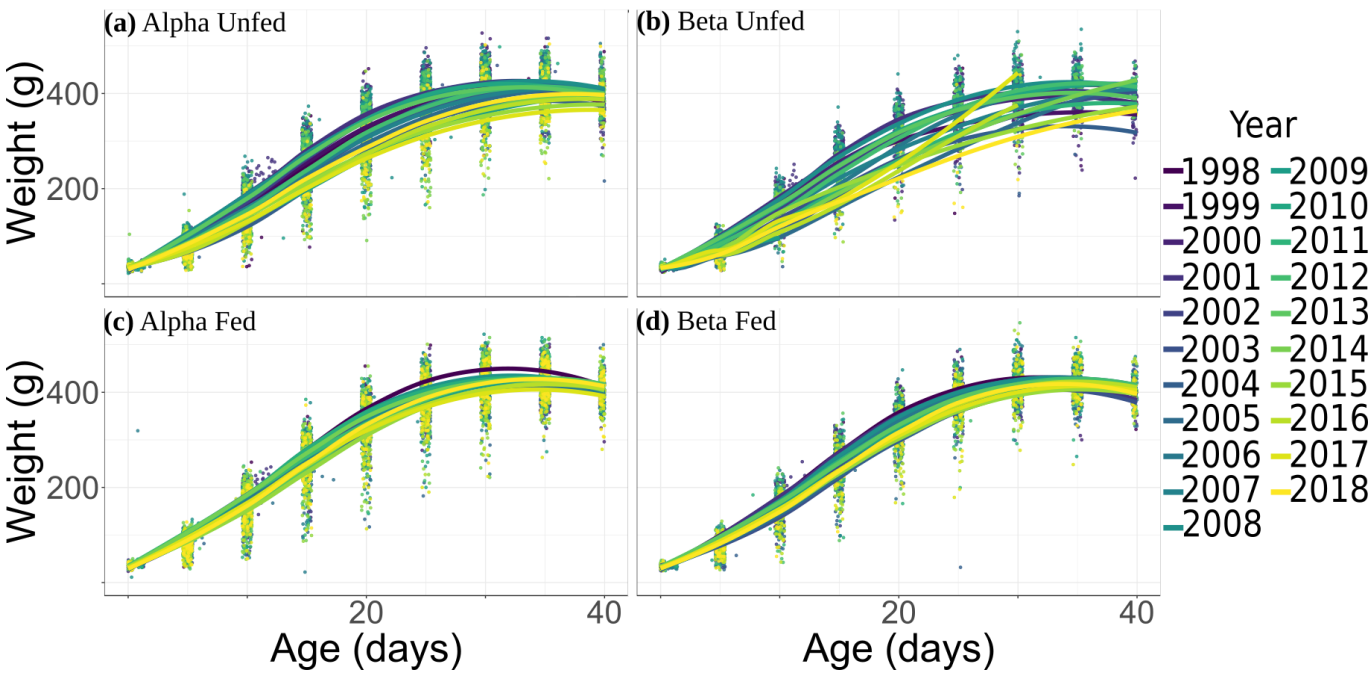
*Effect only apparent under warm air temperatures and when compared to cold or warm sea-surface temperatures under the same conditions. Model predictions suggest air temperatures have the largest impact.

Figure Legends

Figure 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 Supplementary File figure S2 for a plot of the unified Richards curves fit to the data across years (Supplementary File Fig. S2 A, B, C, D)

Figure 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 Supplemental Table 15 for full model details.

Figure 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 prelaying period are displayed. See Supplementary File Table S13 for full model details.



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696 **Figure 1**

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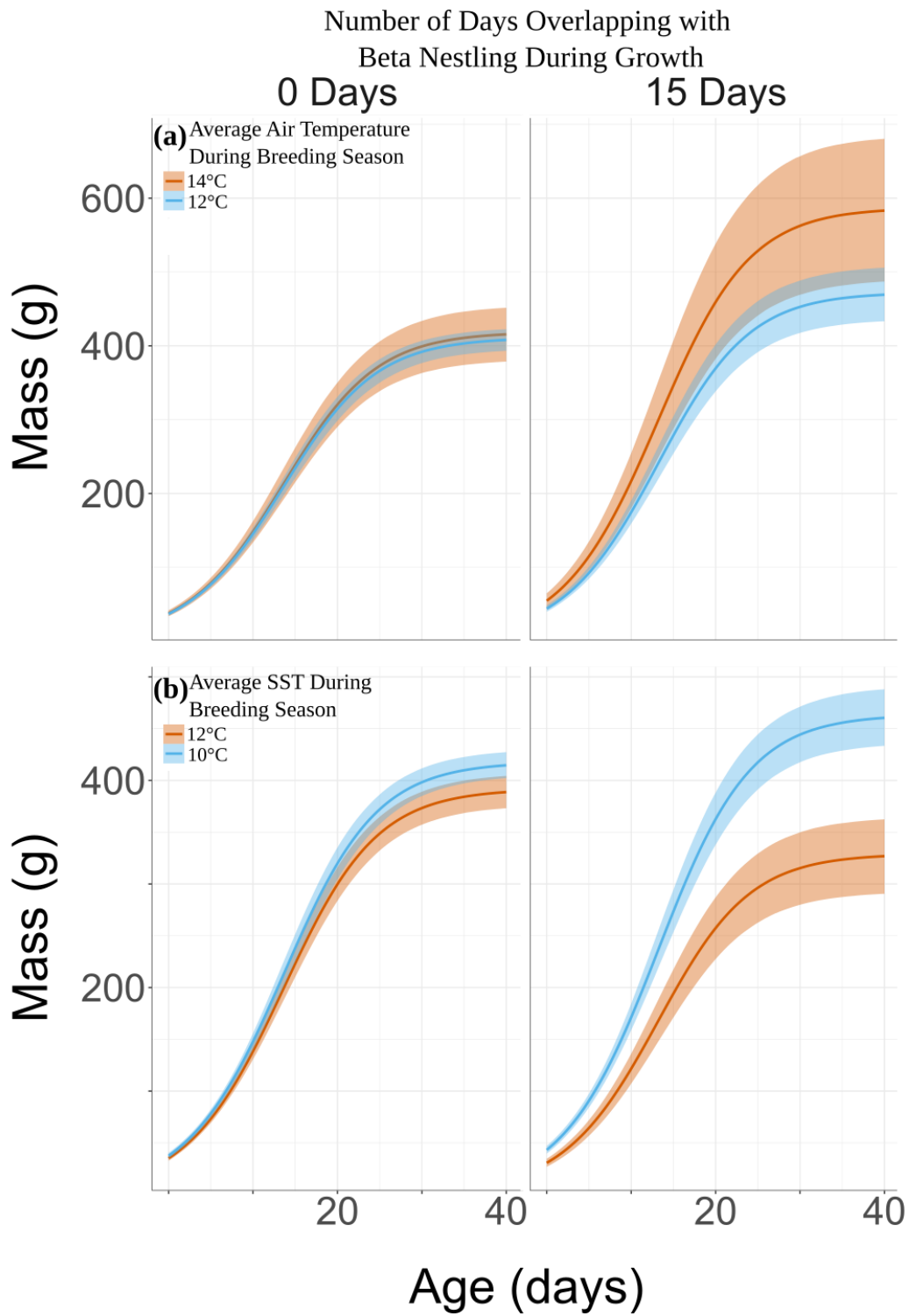
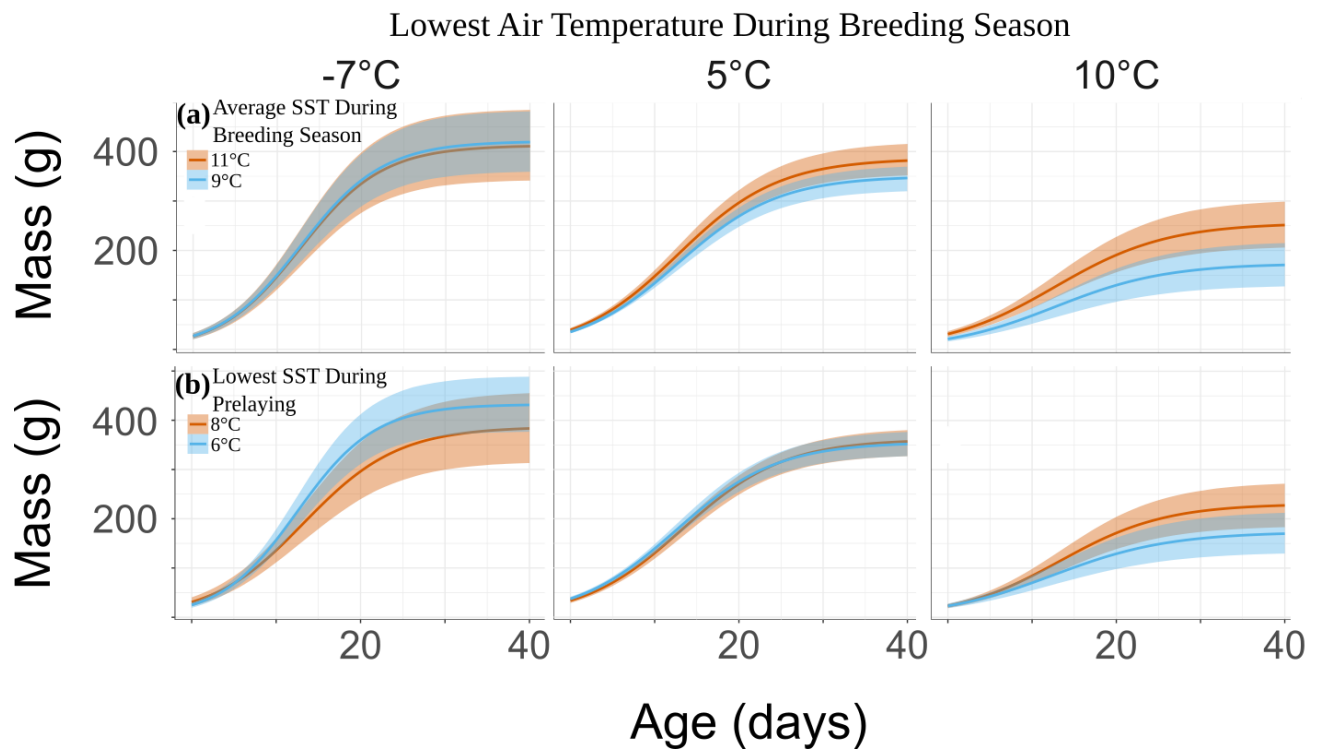


Figure 2



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712 **Figure 3**