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1 **Environmental conditions variably affect growth across the breeding season in a subarctic**
2 **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.

20 **Abstract**

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

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

40 **Introduction**

41 Ongoing global changes are affecting the thermal environment and resource availability for
42 many species across the globe (Intergovernmental Panel on Climate Change, 2018). One

43 important consequence of these abiotic changes is the altered development and growth of
44 offspring. Environmental conditions during early-life can affect an organism's phenotype and
45 fitness (Bateson 1979; Cooper and Kruuk 2018; English et al. 2016; Lindström 1999; Metcalfe
46 and Monaghan 2001). For example, early-life growth traits often predict adult size (Huchard et
47 al. 2014; van Gils et al. 2016), a trait that is frequently under directional selection (Kingsolver
48 and Diamond, 2011). How global environmental change affects fitness may depend on the
49 contribution of the early-life environment to growth, and early-life traits to adult fitness.

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

57 Whereas resources drive organismal growth, temperature determines the efficiency of
58 metabolic processes (Angilletta 2009). As such, temperature extremes may impact the rate of
59 growth and development of tissues. While endothermic animals can regulate their body
60 temperature, thermoregulation often involves trade-offs in energy allocation (Dmitriew 2011).
61 To reduce the energy expenditure of thermoregulation and limit the impacts of unfavourable
62 temperatures, some species may anticipate stressful conditions and either slow development to
63 wait for suitable conditions, or accelerate development to reach maturity earlier at a smaller size
64 (Brannelly et al. 2019; Emlen et al. 1991). However, because of genetic, environmental or
65 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

89 by environmental windows earlier in the breeding season than the asymptote (H1) because the
90 maternal environment during prelaying may influence egg size and early growth (Williams
91 2012). We expected cold sea-surface temperatures to be associated with large, fast-growing
92 nestlings because these conditions correlate with high reproductive success for Middleton's
93 kittiwakes due to increases in capelin *Mallotus villosus* abundance (H2.1; Hatch 2013). In years
94 with warmer sea-surface temperatures, there is a notable reduction in the proportion of capelin in
95 the kittiwake diet and kittiwakes tend to forage on a higher proportion of herring *Clupea pallasii*,
96 invertebrates (e.g. Euphausiidae, Copepoda, Cephalopoda: Gonatidae), myctophids
97 Myctophidae, sablefish *Anoploploma fimbria*, salmon *Oncorhynchus* and sand lance *Ammodytes*
98 *hexapterus* (Hatch 2013). We assumed that small and slow-growing nestlings were indicators of
99 a stressful thermal or resource environment. We expected that warmer air temperatures would be
100 associated with improved growth because current air temperature conditions are below the
101 thermal neutral zone of nestling kittiwakes (H2.2; Bech et al. 1984). Nestlings become
102 homeothermic at 6-8 days of age so warmer temperatures might improve growth directly by
103 providing a better thermal environment or indirectly by allowing parents to spend less time
104 brooding and more time foraging (Hatch et al. 2020). We predicted that fed nestlings would be
105 less affected by air temperatures because they might have had more energy available for thermal
106 regulation and growth (H2.3). Finally, because black-legged kittiwakes exhibit facultative
107 siblicide, we expected the growth of first-hatched nestlings to depend on how long first-hatched
108 nestling shared a nest with a second-hatched nestling (Merkling et al. 2016; H3).

109 **Materials and methods**

110 **Black-legged kittiwake colony and environmental variation**

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

120 Nests are checked twice daily (9:00 and 18:00 H) throughout the season to record laying
121 and hatching. Once hatched, nestlings were weighed every 5 days from hatching to 40 days (i.e.
122 close to fledging). Within a brood, eggs hatch asynchronously with an average difference of 1.64
123 days between the first and second laid egg (Merkling et al. 2014). In each year of the study, the
124 first hatched (“alpha”) and second hatched (“beta”) nestlings are marked with a nontoxic colour
125 marker to distinguish nestling rank. Mass is weighed to the nearest 0.1 g using an electronic
126 scale. Several experiments have been conducted on the nests in the past (e.g. Merkle et al.
127 2014, 2016), so we excluded data from any nestlings that have been experimentally manipulated
128 (~9.1% of breeding attempts excluded, beyond food supplementation).

129 **Predictor variables**

130 We evaluated sea-surface temperature and air temperature as environmental variables that
131 potentially influence nestling growth. Air temperature data were collected from the Middleton
132 Island airport weather station (~2 km from the kittiwake radar tower;
133 <https://www.ncdc.noaa.gov/cdo-web/cart>). Version 2 of the advanced very high-resolution

134 dataset (AVHRR) daily sea-surface temperature data was collected from the National Oceanic
 135 and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC;
 136 <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.OISST/.version2/.AVHRR/.sst/>). All
 137 pixels within a 100 km radius of Middleton Island were averaged each day for sea-surface
 138 temperatures within the region.

139 **Statistical Analyses**

140 **Baseline Models**

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

$$148 \quad W = A \left(1 + (d - 1) \cdot \exp \left(\frac{-k(t - T)}{d^d / (1 - d)} \right) \right)^{1/(1-d)} + \varepsilon, \quad (1)$$

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

$$d \sim 1$$

149 where A is the asymptote or maximum size reached during growth in grams, k is the maximum
 150 relative growth rate (absolute maximum growth rate in grams per day when multiplied by the
 151 asymptote), d affects the shape of the growth curve (sigmoid when greater than 0), T is the age

152 in days at maximum growth, t is the age in days of a nestling, ε is a vector of the residual effects,
153 I is a vector of individual effects, Y is a vector of hatch-year effects, and $Z_{1,2}$ correspond to
154 identity matrices for individual and year effects respectively. Additionally, we estimated the
155 correlation among all non-linear parameters (A , k , T) at the individual and annual level within the
156 model. We only estimated the shape parameter (d) at the population level. To help with
157 convergence, we estimated the asymptote parameter as two orders of magnitude lower and the
158 growth rate parameter as two orders of magnitude higher by multiplying or dividing the
159 parameter within the unified Richards curve, respectively. We used normal priors with a mean of
160 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
161 rate (k), inflection point (T), and shape parameter (d). We used the default half-Student_ t
162 distribution priors with a mean of 0, degrees of freedom of 3, and a standard deviation that is
163 equal to the standard deviation of the response variable (W ; nestling weight) for estimates of the
164 individual (I), annual (Y) and residual (ε) standard deviation. Details of a similar model we use to
165 evaluate whether there are trends in growth parameters across years are included in
166 Supplementary File S1.

167 **Hypotheses 1: Timing of environmental predictors of growth**

168 We performed sliding window analyses using the R package ‘climwin’ (van de Pol et al., 2016).
169 A sliding window analysis identifies a time window for which an environmental variable of
170 interest best explains variation in a measured biological trait. We used relative windows that
171 assume each individual record will be impacted by climate at different times relative to a
172 biological observations' timing. The sliding window analysis varies the start and duration of
173 windows in increments of days and compares both linear and quadratic relationships between the
174 mean, minimum, and maximum values of climatic variation for a given time window and

175 individual estimates of model parameters. The calculation of individual growth parameters and
176 our sliding-window model comparison are in the Supplementary File S1.

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

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

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

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

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

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

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

$$d \sim 1$$

187 where X is a matrix of the predictor variables for each parameter (the observed sliding window
188 values specific to each individual), and b_A , b_k and b_T are vectors of the fixed effects specific to
189 the asymptote, maximum growth rate, and timing of maximum growth (effects of windows of
190 sea-surface and air temperature identified by the sliding window analysis). We ran models for

191 sea-surface and air temperature separately. Finally, we ran a model where we only retain the
192 fixed effects that did not span zero in sea-surface and air temperature models and combine them
193 into one model. We chose this approach to evaluating our effects in a final model, rather than an
194 information criterion approach, to restrict the combination of window-effects evaluated and keep
195 model choice simple to reduce computation time. This final model included the fixed effects for
196 each parameter and an additional interaction effect between air and sea-surface temperature
197 windows if we retained both an air and sea-surface temperature window for a parameter (A , k , T).
198 Our approach to interpreting interactions is detailed in the Supplementary File S1. Priors for our
199 environmental models were identical to those used in initial growth models above with the
200 addition of a Student-t prior for fixed effect coefficients with a mean of 0, a standard deviation of
201 5, and 10 degrees of freedom.

202 **Hypothesis 3: Interaction of competition and environmental conditions**

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

210 **Results**

211 **Models of nestling growth and trends over time**

212 The dataset included 8198 records of mass from 1190 unfed alpha nestlings ($\bar{n} = 6.8/\text{nestling}$),
213 3522 records of mass from 788 unfed beta nestlings ($\bar{n} = 4.4/\text{nestling}$), 7415 records of mass

214 from 994 fed alpha nestlings ($\bar{n} = 7.5/\text{nestling}$), and 4089 records of mass from 676 fed beta
215 nestlings ($\bar{n} = 6.1/\text{nestling}$). Growth parameters varied among individuals and years, and the
216 timing of maximum growth and maximum growth was correlated in all models (Supplementary
217 Table S1). In more recent years unfed alpha, unfed beta, and fed beta nestlings had on average
218 lighter asymptotes than at the beginning of the study (Supplementary File Tables S2-3, S5).
219 However, there were no linear or quadratic trends over time for the fed alpha nestlings'
220 asymptote (Supplementary File Tables S4). All nestlings, including fed alpha nestlings, tended to
221 grow more slowly and exhibit maximum growth at an older age in more recent years when
222 compared to nestlings growing in early years of the study (Fig. 1; Supplementary File Tables S2-
223 5). Increasing overlap with a beta nestling in the nest correlated with a faster maximum growth
224 rate and earlier timing of maximum growth for alpha nestlings (Supplementary File Table S6,
225 S7).

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

227 Average sea-surface and air temperatures varied among years (Supplementary File Tables S10,
228 S11; Supplementary File Figs. S11, S12). The average sea-surface temperature during the
229 breeding season increased by 0.43°C over the course of the study (CI = $[0.05^{\circ}\text{C}, 0.81^{\circ}\text{C}]$; or
230 0.02°C per year, CI = $[0.002^{\circ}\text{C}, 0.04^{\circ}\text{C}]$) and air temperatures during the breeding season
231 increased by 0.74°C (CI = $[0.32^{\circ}\text{C}, 1.15^{\circ}\text{C}]$; or 0.04°C per year, CI = $[0.02^{\circ}\text{C}, 0.05^{\circ}\text{C}]$).

232 **Hypotheses 1: Timing of environmental predictors of growth**

233 For both air and sea-surface temperatures, our sliding window analysis tended to identify
234 climatic windows during the prelaying period as the best predictors of maximum growth rate and
235 timing of maximum growth (Table 2). The time window of climatic variation that predicted the
236 asymptote varied but generally included the growth period or encompassed the entire breeding

237 season (Table 2; Supplementary File Table S8). We identified fewer windows from the sliding
238 window analysis that predicted growth variation for the food-supplemented nestlings (Table 2;
239 Supplementary File Table S8). Our environmental models of food-supplemented nestling growth
240 only included a window of air temperature during the prelaying period (days) that was a
241 predictor of the timing of maximum growth. Temperatures within each window that we
242 identified with our sliding window analysis increased throughout the study (Supplementary File
243 Figs. S3-S8).

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

245 Warmer maximum air temperatures and colder minimum sea-surface temperatures throughout
246 the season correlated with heavier asymptotes in unfed alpha nestlings (Fig. 2; Supplementary
247 File Table S12; Table 3). In contrast to alpha nestlings, breeding seasons with a low minimum air
248 temperature tended to result in faster-growing and larger unfed beta nestlings (Fig. 3 A, B; Table
249 3; Supplementary File Table S13). The average sea-surface temperature of the season had a
250 small effect on the growth of a beta nestling if the season's minimum air temperature was cold.
251 Nestlings that grew in a warm minimum air temperature season and a warm average sea-surface
252 temperature season grew faster and to a larger asymptote than those that grew in a season with
253 warm minimum air temperature and a cold average sea-surface temperature (Fig. 3A). Warm
254 minimum sea-surface temperatures during prelaying correlated with slow growth and light
255 asymptotes when the minimum air temperature of a season was low, but fast-growing nestlings
256 when the minimum air temperature of a season was high (Fig 6B).

257 Food-supplemented alpha nestlings that grew in seasons with lower minimum air
258 temperatures during the prelaying and incubation periods exhibited maximum growth at a

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

261 **Hypothesis 3: Interaction of competition and environmental conditions**

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

268 Controlling for nestling competition revealed some nuance to the effects of temperatures
269 on unfed alpha nestling growth. Increases in days of overlap with a beta nestling resulted in
270 heavy alpha nestlings in seasons with warm average air temperatures, but light alpha nestlings in
271 seasons with warmer average sea-surface temperatures (Fig. 2). Overlap models demonstrated
272 that warmer average air temperature and colder minimum air temperatures during prelaying
273 resulted in fed alpha nestlings that exhibited maximum growth at a younger age, but this effect
274 was weaker the more days an alpha nestling overlapped with a beta (Supplementary File Fig. S10
275 A, B). Further, controlling for overlap with a beta nestling in food supplemented alpha nestlings
276 revealed an association of a warmer average sea-surface temperature with lighter asymptotes in
277 fed alpha nestlings (Supplementary File Fig. S10 C).

278 **Discussion**

279 We examined the effects of thermal conditions on kittiwake nestling growth in alpha and beta
280 nestlings, a portion of which were food supplemented to ease dietary constraints. Our results
281 were concordant with carry-over effects from the prelaying period impacting growth rate

282 parameters. In contrast, asymptotic size was largely dependent on weather variation during
283 growth. Avian maternal effects are typically strong right after hatching and subsequently weaken
284 during development (Williams 2012; Williams and Groothuis 2015). Therefore, we expected the
285 prelaying environment to affect traits expressed earlier during growth (maximum growth rate and
286 timing of maximum growth) while we expected environmental effects during the growth period
287 to influence traits expressed later during growth, like the asymptote (P1.1 and P1.2). Our sliding
288 window analysis frequently, but not always, identified environmental variation in the prelaying
289 period to best predict the timing of maximum growth and the maximum growth rate, while
290 windows that best predicted the asymptote tended to occur during the growth period or over the
291 entirety of the breeding season (Table 2). Weather during the prelaying period might influence
292 food resources available during growth, or carry-over effects might impact parental behaviour
293 during growth. Kruuk et al. (2015) and Marques-Santos and Dingemanse (2020) used a sliding
294 window approach and found that weather conditions during the growth period likely influenced
295 the 14-day masses of nestlings (which might be comparable to our asymptote parameter) in
296 superb fairy-wrens *Malurus cyaneus* and great tits *Parus major*. However, Kruuk et al. (2015)
297 also identified windows before the growth period that influenced 14-day mass. Future studies
298 should investigate when and how environmental conditions affect growth traits in a diversity of
299 species and locations to confirm that early and late breeding season environments most strongly
300 affect traits early and late in ontogeny, respectively.

301 **Sea-surface temperature effects on kittiwake nestlings**

302 Altered sea-surface temperatures can change the phenology, distribution and abundance of prey
303 species for seabirds and decrease the growth of nestlings (e.g. Hedd et al. 2002). Because our
304 windows of sea-surface temperature occur during the nestling growth phase for alpha nestlings,

305 we suspect the smaller asymptotes indicate lower availability of preferred prey species to
306 kittiwakes during the growth period (decreases in proportion of capelin in diet). As warmer sea-
307 surface conditions are related to an increased proportion of less favourable prey sources in the
308 kittiwake diet (herring, invertebrates, myctophids, sablefish, salmon, and sand lance) on
309 Middleton Island (Hatch 2013), we predicted that warmer sea-surface temperatures would
310 correlate with slower growth, smaller asymptotes, and older ages at maximum growth (P2.1). We
311 observed a slight decrease in alpha nestling asymptotes when sea-surface temperatures are on
312 average warmer during the growth period. In black-legged kittiwakes on Middleton Island
313 warmer years correlate with a decrease in productivity, a decrease in preferred prey (capelin),
314 and an increase in foraging distance of adult birds (Hatch 2013; Osborne et al. 2020). Kittiwakes
315 on Middleton seem to have to search a larger area for profitable foraging areas in warm years but
316 can stay close to the colony in cold years when capelin are available close to the colony
317 (Osborne et al. 2020).

318 **Air temperature effects on nestling kittiwakes**

319 For cold-climate species, warmer air temperatures may be beneficial because they may decrease
320 nestling energy expenditure on thermoregulation and parental energy expenditure on brooding
321 (e.g., McKinnon et al. 2013). We expected that colder air temperatures would slow growth and
322 decrease the asymptotic size (P2.2). However, our results indicated that warmer air temperatures
323 correlated with alpha nestlings that grow to a heavier asymptote (Fig. 2; Supplementary File
324 Table S12) yet slower-growing beta nestlings that reach a lighter asymptote (Fig. 3A, B;
325 Supplementary File Table S13). Because the air temperature windows identified for the alpha
326 and beta nestlings are broad, encompassing most of the breeding season, it is challenging to
327 attribute air temperature variation to a particular breeding stage. Air temperature effects could

328 represent direct effects on nestling growth or indirect effects via parental foraging. In wild bird
329 populations, warmer air temperatures can correlate with fast-growing and heavy nestlings and
330 slow-growing small nestlings (e.g. Andrew et al. 2017; Cunningham et al. 2013; Hiraldo 1990).
331 Nestlings that experience temperatures outside their thermal limit will experience adverse
332 effects, and different temperature changes experienced by populations and variation among
333 species' thermoregulatory ability likely explain contrasts among studies (reviewed in Sauve et al.
334 2021). Currently, warmer air temperatures appear to improve alpha nestlings' growth and may
335 continue to do so until ambient temperatures exceed the thermal neutral zone for kittiwake
336 nestlings, between 33⁰ C and 35⁰ C for newly hatched nestlings (Bech et al. 1984).

337 In contrast to patterns found in alpha nestlings, the effect of the minimum air temperature
338 window on beta nestlings did not follow our prediction that warmer minimum air temperatures
339 result in heavy and fast-growing nestlings (P2.2). It seems unlikely that the air temperature effect
340 on beta nestling growth resulted from a direct effect because air temperatures did not exceed the
341 thermal neutral zone of nestling kittiwakes (Bech et al. 1984). However, the negative effect of
342 warming on growth could represent an indirect effect or predictor of food resources, parental
343 care, or egg hormones. Contrasting impacts of warmer air temperature could suggest increased
344 parental investment in the alpha nestling and negative impacts of sibling aggression towards the
345 beta nestling under difficult foraging conditions (Drummond 2001). The amount of parental care
346 provided to the beta nestlings might depend on environmental conditions. In many species,
347 parents overproduce young and use various brood reduction mechanisms to match local
348 environmental conditions (Braun and Hunt 1983; Mock and Parker, 1997). Food availability or
349 other environmental cues, such as effects of sea-surface temperature on beta nestlings discussed

350 below, could also alter parental care during nestling growth to allow or prevent brood reduction.
351 (e.g. parental compensation, Shizuka and Lyon 2013).

352

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

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

366 Because sea-surface temperature is often related to the level of food resources available for
367 seabirds and is related to food conditions for kittiwakes on Middleton (Furness 2016; Hatch
368 2013), we expected nestling kittiwakes experiencing cold sea-surface temperatures during
369 growth to be less affected by air temperature variation (P2.3.2). The interactions between air and
370 sea-surface temperature do not support this prediction for unfed alpha or beta nestlings. In fact,
371 warmer air temperatures predict large alpha nestlings, and in unfed beta nestlings warmer sea-

372 surface temperatures are associated with larger, faster-growing nestlings under warm air
373 temperature conditions.

374 The effect of sea-surface temperature on unfed beta nestlings was dependent on the
375 minimum air temperature of the breeding season. Under cold minimum air temperatures, warmer
376 average sea-surface temperatures during the breeding season had little effect on beta nestlings'
377 growth curve. However, when air temperatures are warm, warmer average sea-surface
378 temperatures during the season result in beta nestlings that grew slightly faster to a larger size
379 relative to nestlings that grew in a season with colder average sea-surface temperatures (Fig. 3A).
380 An observation of a similar interaction between air and the sea-surface temperatures occurred for
381 minimum sea-surface temperatures during the prelaying period (Fig. 3B). Interpreting the
382 consequences of warmer sea-surface temperature on nestling growth is more challenging for beta
383 nestlings than alpha nestlings. Perhaps cues from air or sea-surface temperature during any of
384 these periods are informative for improving nestling growth conditions (Marshall and Uller
385 2007). Alternatively, better growth of beta nestlings in warmer sea-surface temperature
386 conditions could represent an effect of “high-quality” parents (Coulson and Porter 1985). Parents
387 that successfully raised beta nestlings in difficult warm environmental conditions might be
388 parents that are investing extensive effort into both the alpha and beta nestlings (Weimerskirch
389 1992; Winkler 1987).

390 **Competition among siblings**

391 Competition among siblings might make them more sensitive to environmental effects. Whereas
392 some alpha nestlings compete with a beta nestling throughout most of the growth phase, others
393 (~43%) never compete with a beta sibling because of reduced clutches or early life mortality of
394 beta nestlings. We expected alpha nestlings to be more susceptible to environmental effects the

395 longer they had to share a nest with a sibling (H3). We found that increasing overlap with a beta
396 nestling indeed amplified the positive effects on growth of a warmer air temperature season and
397 the negative effects of warmer sea-surface temperatures (P3; Fig 2 A, B). For fed alpha nestlings,
398 more overlap with a beta nestling dampened the overall effects of the average air temperature of
399 a season and the minimum air temperature during the prelaying period on the timing of
400 maximum growth (Supplementary File Fig. S10 A, B). Further, when we accounted for sibling
401 competition, our model included a negative effect of warmer sea-surface temperatures on fed
402 alpha nestlings' asymptote (Supplementary File Fig. S10 C). Our models of fed alpha nestlings
403 suggest effects that are small and difficult to explain and might be the result of cues used by
404 parents in warm conditions that change alpha nestling growth directly, or the influence of
405 competition with beta nestlings on alpha nestlings.

406 **Implications for kittiwakes under climate change and future directions**

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

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

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

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451 **Conflicts of interest/Competing interests**

452 The authors declare that they have no conflict of interest.

453 **Ethics Approval**

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

457 **Consent to participate**

458 Not applicable.

459 **Consent for publication**

460 Not applicable.

461 **Availability of data and material**

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

463 **Code availability**

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

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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

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643 **Table 2:** Environmental windows retained in our environmental analysis. Windows that
 644 overlapped multiple categories are indicated by a slash (e.g. Incubation/Growth indicates a
 645 window that spans incubation & growth). Displayed are windows identified for air and sea-
 646 surface temperature (SST) for kittiwakes that were not food-supplemented and those that were
 647 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*	Prelying	Prelying	
Beta		Breeding Season*	Prelying*	Prelying	
Air Temperature					
Alpha		Breeding Season*	Prelying	Prelying	
Beta		Incubation/ Growth	Prelying	Breeding Season*	
Food Supplemented					
SST		Asymptote	Max Growth Rate	Timing of Max Growth	
Alpha		Growth	Breeding Season	Prelying	
Beta		None	Prelying	Breeding Season	
Air Temperature					
Alpha		Growth	Growth	Prelying/ Incubation*	
Beta		None	Prelying	Prelying	

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

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

	Alpha		Fed	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	

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

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672 **Figure Legends**

673 **Figure 1:** Raw annual growth curves for each year of the study for A) Alpha unfed kittiwakes,
674 B) Beta unfed kittiwakes, C) Alpha fed kittiwakes, and D) Beta unfed kittiwakes. Points indicate
675 individual weight measurements of nestlings. Points and loess curves are coloured by year of
676 study. In two years (2016 & 2017) no mass measurements beyond 30 days of age were taken for
677 beta nestlings. See Supplementary File figure S2 for a plot of the unified Richards curves fit to
678 the data across years (Supplementary File Fig. S2 A, B, C, D)

679 **Figure 2:** Interaction between the number of days an unfed alpha nestling overlapped its growth
680 with abeta sibling and a) the average air temperature in a season and b) the average sea-surface
681 temperature of a season. See Supplemental Table 15 for full model details.

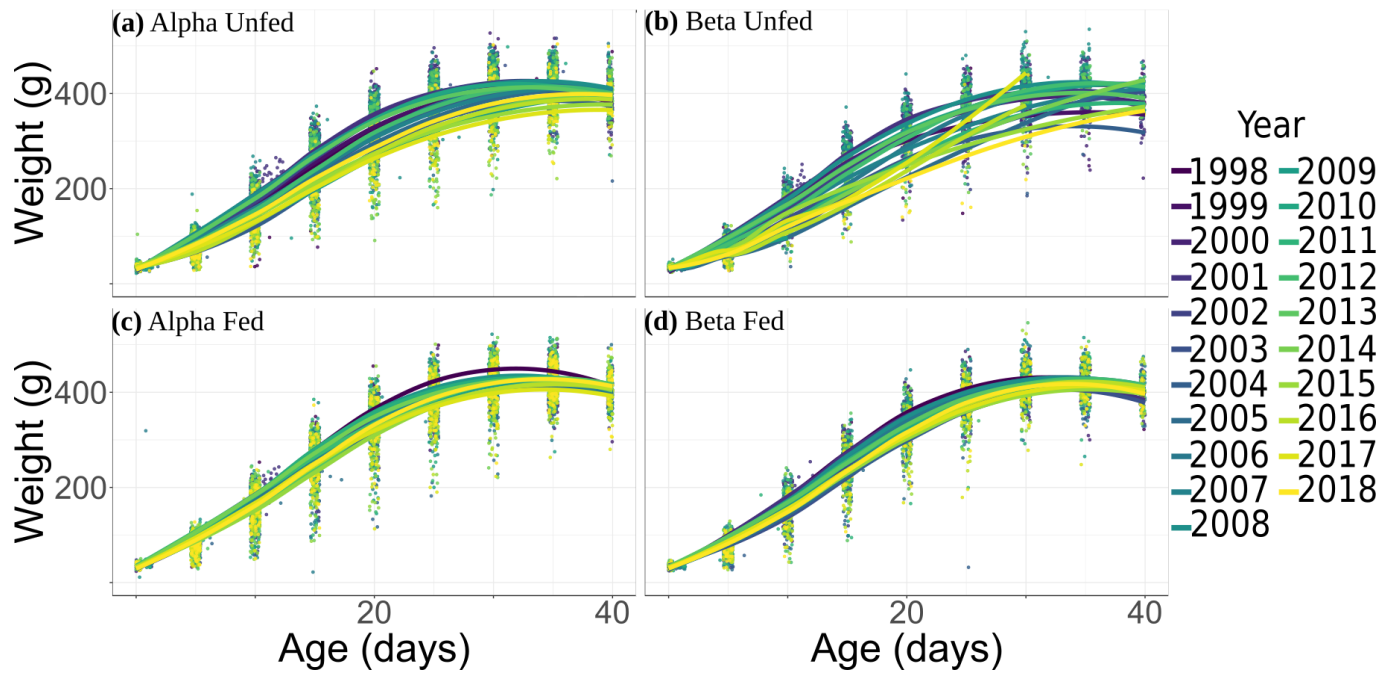
682 **Figure 3:** Impacts of variation within air temperature and sea-surface temperature (SST)
683 windows on the growth of unfed beta nestlings. In the display of interactions only the range of
684 SST and air temperature that occurred in a given year are shown. Both A & B display an effect
685 of different minimum air temperatures from a particularly cold minimum temperature breeding
686 season on the left most panel to a warm minimum air temperature breeding season on the right.
687 Within each panel effects of A) different average sea-surface temperatures during the breeding
688 season or B) the minimum sea-surface temperature during the prelaying period are displayed.
689 See Supplementary File Table S13 for full model details.

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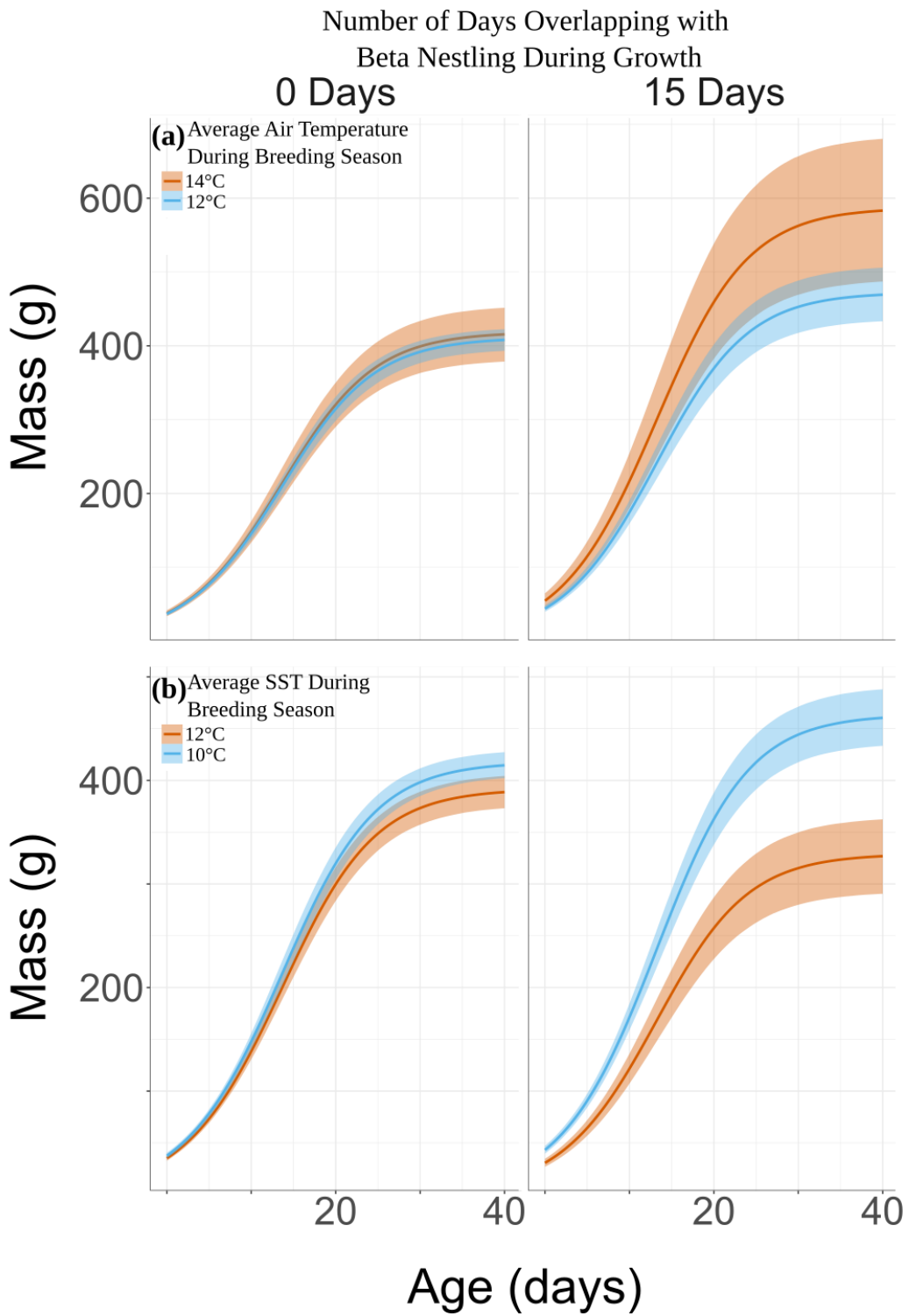
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696 **Figure 1**

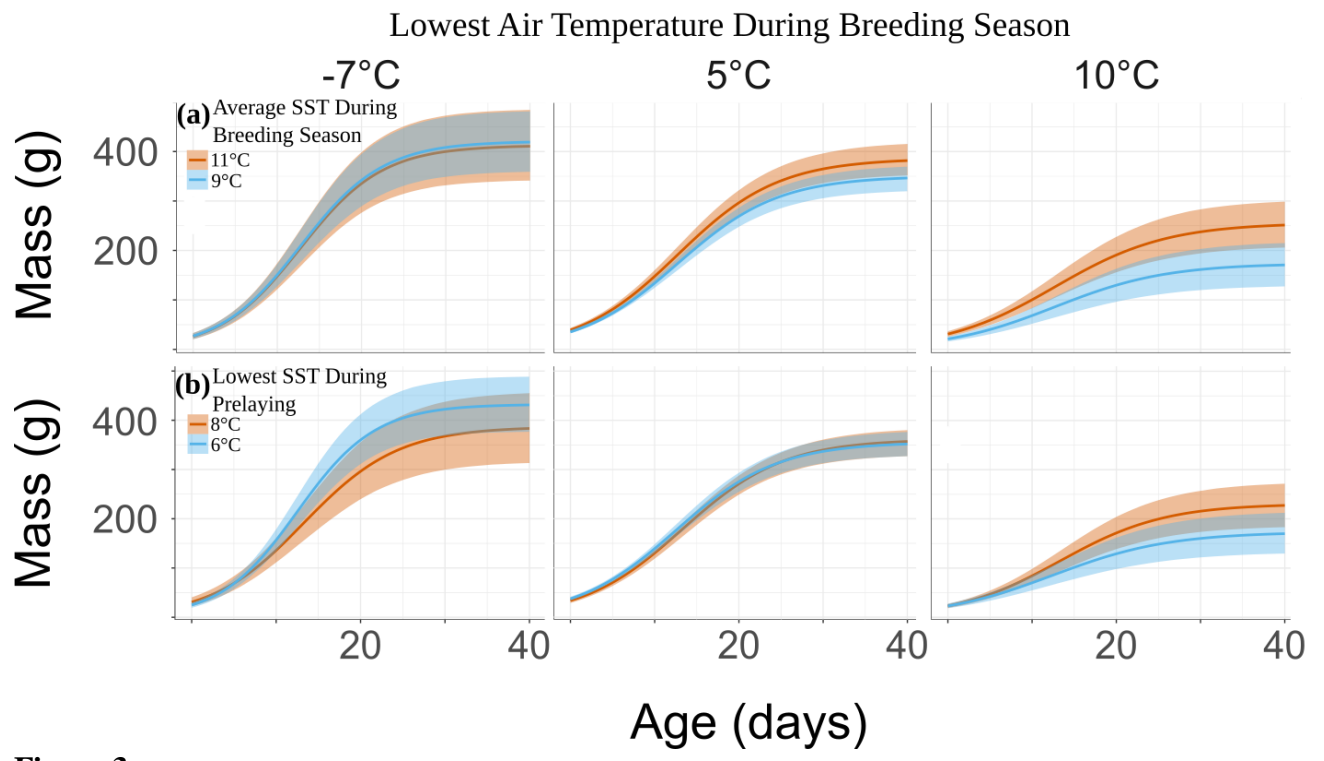


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708 **Figure 2**

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 712 **Figure 3**