



Royal Netherlands Institute for Sea Research

This is a pre-copyedited, author-produced version of an article accepted for publication, following peer review.

Lameris, T.K.; Tomkovich, P.S.; Johnson, J.A.; Morisson, R.I.G.; Tulp, I.; Lisovski, S.; DeCicco, L.; Dementyev, M.; Gill, R.E.; ten Horn, J.; Piersma, T.; Pohlen, Z.; Schekkerman, H.; Soloviev, M.; Syroechkovsky, E.E.; Zhemchuzhnikov, M.K. & van Gils, J.A. (2022). Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely mitigated by increasing temperatures. *Glob. Chang. Biol.* 28(3): 829-847. DOI: 10.1111/gcb.16025

Published version: <https://dx.doi.org/10.1111/gcb.16025>

NIOZ Repository: <http://imis.nioz.nl/imis.php?module=ref&refid=348092>

[Article begins on next page]

The NIOZ Repository gives free access to the digital collection of the work of the Royal Netherlands Institute for Sea Research. This archive is managed according to the principles of the [Open Access Movement](#), and the [Open Archive Initiative](#). Each publication should be cited to its original source - please use the reference as presented.

When using parts of, or whole publications in your own work, permission from the author(s) or copyright holder(s) is always needed.

1 **Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely**
2 **mitigated by increasing temperatures**

3 Running title: mismatches reduce growth in shorebird chicks

4 Thomas K. Lameris^{1*}, Pavel S. Tomkovich², James A. Johnson³, R.I. Guy Morrison⁴, Ingrid Tulp⁵,
5 Simeon Lisovski⁶, Lucas DeCicco³, Maksim Dementyev⁷, Robert E. Gill Jr.⁸, Job ten Horn¹, Theunis
6 Piersma^{1,9}, Zachary Pohlen³, Hans Schekkerman¹⁰, Mikhail Soloviev⁷, Evgeny E. Syroechkovsky¹¹,
7 Mikhail K. Zhemchuzhnikov¹, Jan A. van Gils^{1,9}

8 **ORCID ID's:** Thomas K. Lameris: [0000-0001-7023-3406](https://orcid.org/0000-0001-7023-3406); Pavel S. Tomkovich: [0000-0002-1563-](https://orcid.org/0000-0002-1563-2196)
9 [2196](https://orcid.org/0000-0002-1563-2196); James A. Johnson: [0000-0002-2312-0633](https://orcid.org/0000-0002-2312-0633); R.I.Guy Morrison: [0000-0003-3964-2118](https://orcid.org/0000-0003-3964-2118); Ingrid
10 Tulp: [0000-0001-6002-1741](https://orcid.org/0000-0001-6002-1741); Simeon Lisovski: [0000-0002-6399-0035](https://orcid.org/0000-0002-6399-0035); Lucas DeCicco: [0000-0001-](https://orcid.org/0000-0001-9477-3124)
11 [9477-3124](https://orcid.org/0000-0001-9477-3124); Robert E. Gill. Jr.: [0000-0002-6385-4500](https://orcid.org/0000-0002-6385-4500); Theunis Piersma: [0000-0001-9668-466X](https://orcid.org/0000-0001-9668-466X); Hans
12 Schekkerman: [0000-0003-3127-4832](https://orcid.org/0000-0003-3127-4832); Mikhail Soloviev: [0000-0003-4040-1477](https://orcid.org/0000-0003-4040-1477); Mikhail K.
13 Zhemchuzhnikov: [0000-0003-3838-6167](https://orcid.org/0000-0003-3838-6167); Jan A. Van Gils: [0000-0002-4132-8243](https://orcid.org/0000-0002-4132-8243)

14 1 NIOZ Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands

15 2 Zoological Museum, MV Lomonosov Moscow State University, Moscow, Russia.

16 3 Migratory Bird Management, US Fish and Wildlife Service, Anchorage, Alaska, USA

17 4 National Wildlife Research Centre, Environment and Climate Change Canada, Ottawa, Ontario,
18 Canada

19 5 Wageningen Marine Research, Wageningen University, IJmuiden, The Netherlands

20 6 Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Potsdam, Germany

21 7 Department of Vertebrate Zoology, Lomonosov Moscow State University, Moscow, Russia

22 8 U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA

23 9 Conservation Ecology Group, Groningen Inst. for Evolutionary Life Sciences (GELIFES),
24 University of Groningen, Groningen, the Netherlands

25 10 Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands

26 11 BirdsRussia, Moscow, Russia

27 *corresponding author: thomaslameris@gmail.com, +31633911043

28 In seasonal environments subject to climate change, organisms typically show phenological changes.
29 As these changes are usually stronger in organisms at lower trophic levels than those at higher trophic
30 levels, mismatches between consumers and their prey may occur during the consumers' reproduction
31 period. While in some species a trophic mismatch induced reductions in offspring growth, this is not
32 always the case. This variation may be caused by relative strength of the mismatch, or by mitigating
33 factors like increased temperature reducing energetic costs. We investigated the response of chick
34 growth rate to arthropod abundance and temperature for six populations of ecologically similar
35 shorebirds breeding in the Arctic and sub-Arctic (four subspecies of Red Knot *Calidris canutus*, Great
36 Knot *C. tenuirostris* and Surfbird *C. virgata*). In general, chicks experienced growth benefits
37 (measured as a condition index) when hatching before the seasonal peak in arthropod abundance, and
38 growth reductions when hatching after the peak. The moment in the season at which growth reductions
39 occurred varied between populations, likely depending on whether food was limiting growth before or
40 after the peak. Higher temperatures led to faster growth on average, but could only compensate for
41 increasing trophic mismatch for the population experiencing the coldest conditions. We did not find
42 changes in the timing of peaks in arthropod availability across the study years, possibly because our
43 series of observation was relatively short; timing of hatching displayed no change over the years
44 either. Our results suggest that a trend in trophic mismatches may not yet be evident; however, we
45 show Arctic-breeding shorebirds to be vulnerable to this phenomenon and vulnerability to depend on
46 seasonal prey dynamics.

47 **Key words:** arthropods, Great Knot, Red Knot, shorebirds, Surfbird, trophic mismatch

48 **1. Introduction**

49 As a response to rapid climate warming, many species in seasonal environments are advancing
50 activities such as the onset of reproduction (Post et al., 2018). Organisms at lower trophic levels
51 typically advance their phenology at a faster rate than their consumers (Thackeray et al., 2010, 2016).
52 The difference in response rate can result in trophic mismatches between the consumers' demands and
53 their food resources (Both et al., 2009; Renner & Zohner, 2018; Visser & Gienapp, 2019). Examples
54 include trophic mismatches between bird reproduction and the timing of mass emergence of their
55 insect prey (Kwon et al., 2019; Visser et al., 2004), and between arrival of migratory herbivores and
56 the timing of peak quality of forage plants (Post & Forchhammer, 2008; Lameris et al., 2018). In
57 environments where food is limited outside a narrow period of peak occurrence (Visser et al. 2005),
58 advancements of the food peak can effectively reduce the amount of food available to organisms
59 during periods of high demand, for example, the offspring development stage (Drent & Daan, 1980).
60 The resulting trophic mismatches can impact offspring growth (Doiron et al., 2015; Senner et al.,
61 2017), survival (Lameris et al., 2018; Saalfeld et al., 2021) and recruitment (Reed et al., 2013). Such
62 changes in species interactions due to a warming climate are considered an important threat to animal
63 populations (Ockendon et al., 2014).

64 While an increasing number of studies have identified trophic mismatches for a large suite of
65 species (Renner & Zohner, 2018; Thackeray et al., 2016), there are substantially fewer reports on their
66 impacts on fitness (Visser et al., 2012). Those that have done so indicate large variation in effect size
67 (Knudsen et al., 2011; Visser & Gienapp, 2019). Recently, some studies have revealed mismatches
68 that do not impact fitness (Corkery et al., 2019; Machín et al., 2018; Reneerkens et al., 2016) and in a
69 recent review study, Zhemchuzhnikov et al. (2021) were unable to establish a clear link between the
70 extent of a trophic mismatch and fitness. The absence of a clear relationship between trophic mismatch
71 and population dynamics may be influenced by the large variation in the effect sizes of trophic
72 mismatches. Therefore, further studies to pin down why populations vary in sensitivity to trophic
73 mismatch are needed (Miller-Rushing et al., 2010).

74 In theory, assuming that food is limiting fitness outside peaks in resource availability,
75 reductions in fitness can be expected when the consumer's demands are highest either after or before
76 these peaks (Drent, 2006; Kharouba & Wolkovich, 2020; Perrins, 1970). Many studies on trophic
77 mismatch focus on timing of reproduction, where the mismatch is expressed as the difference between
78 the seasonal time of birth or hatch and the time of a single peak in resource availability (this is the
79 'relative hatch/birth date'). Single resource peaks are probably rather rare, with multiple peaks
80 throughout a season being much more common (e.g. Tulp & Schekkerman, 2008). Still, timing of
81 hatch relative to a peak or period of high resource abundance (including multiple peaks) appears to be
82 an important determinant of fitness (e.g. Reed et al., 2013; Samplonius et al., 2016). In general,
83 highest fitness is reached at hatch dates falling shortly before or coinciding with the peak in resource
84 availability (Fig. 1a), although multiple peaks during the season can drive more complicated patterns
85 in fitness rewards (Machín et al., 2018). Variation in relative hatch date can explain variation in fitness
86 within a population, as well as between populations (Fig. 1a). Assuming the advancement of food
87 peaks in a warming climate, populations with current hatch/birth dates after the food peak will face
88 greater fitness reductions, while populations with current hatch/birth dates before the peak will have
89 some leeway before fitness is reduced (and may even initially benefit from a later relative hatch date).

90 However, food availability is often not the only factor affecting fitness (Visser & Gienapp,
91 2019). For example, it has been suggested that in cold Arctic and alpine environments, growth
92 reductions due to trophic mismatches can be mitigated by positive direct effects of increasing
93 temperature (McKinnon et al., 2013). Below certain threshold levels (Kersten & Piersma, 1987) higher
94 temperatures will reduce the cost of thermoregulation for endotherms such as birds. Especially for
95 precocial chicks that forage independently immediately after hatching, the cost of thermoregulation
96 can be considerable (Bakken et al., 2002; Schekkerman & Visser, 2001). By brooding their offspring,
97 birds can reduce the chicks' costs of thermoregulation (Klaassen et al., 1989) and mitigate the effects
98 of low temperature in the first week(s) after hatching (Schekkerman et al., 2003). An increase in
99 temperature will not only reduce thermoregulatory costs, but also brooding time, allowing precocial
100 chicks and their parents more time to forage. Furthermore, higher temperatures may also increase the

101 activity, availability and detectability of arthropod prey (Schekkerman et al., 2003; Tulp &
102 Schekkerman, 2008), potentially negating the short-term impact of a trophic mismatch. Such
103 mechanisms increase the potential for growth and may (partially) compensate for the impacts of
104 trophic mismatch in a warming climate (Fig. 1b, McKinnon et al., 2013). However, as
105 thermoregulatory costs are only one component of the energy budgets of chicks (Schekkerman &
106 Visser, 2001), the variation therein is probably smaller than the variation in energy intake, which fully
107 depends on prey availability that can vary by more than an order of magnitude on a short timescale
108 (hours to days). A reduction in thermoregulation costs due to higher temperatures may therefore be
109 unlikely to fully compensate for negative effects of trophic mismatch.

110 Arctic-nesting shorebirds represent a particularly suitable system to study response to
111 mismatch and temperature increase, as these birds inhabit a region characterised by low temperatures
112 but yet the highest rates of climate change. Owing to climate feedbacks, the Arctic is warming faster
113 than any other region on the globe (Serreze & Barry, 2011). In the last 50 years, summer temperatures
114 in the Arctic have increased by 1.8°C and the date of snowmelt has advanced by 15.5 days on average
115 (Box et al., 2019). With such steep warming, organisms at low levels in the food chain likely show
116 stronger responses to climate change than anywhere else on Earth. The phenology of arthropod
117 emergence, the primary food for shorebird chicks (Holmes & Pitelka, 1968), is advancing at a higher
118 pace in the Arctic than elsewhere (Post et al., 2018). However, most studied species of Arctic-nesting
119 shorebirds have not adjusted their laying dates (Reneerkens et al., 2016; Saalfeld & Lanctot, 2017;
120 Meltofte et al. 2021, but see Rakhimberdiev et al., 2018), which can result in trophic mismatch (Kwon
121 et al., 2019; Zhemchuzhnikov et al., 2021).

122 In this paper we aim to quantify the response of chick growth to trophic mismatch and
123 temperature in a clade of Arctic and sub-Arctic nesting Calidrine shorebirds (Gibson & Baker, 2012;
124 Thomas et al., 2004) (Fig. 2): Red Knots (*Calidris canutus*), Great Knots (*C. tenuirostris*) and
125 Surf-birds (*C. virgata*). Together, these species have an almost circumpolar distribution, yet breed at
126 different latitudes and elevations, thereby experiencing varying rates of climate change with
127 potentially different impacts on chick growth. Using comparisons between and within populations, we

128 study (1) how populations vary in the response of chick growth to potential trophic mismatch, and (2)
129 whether effects of mismatch can be mitigated by temperature increases. Given that Arctic-nesting
130 shorebirds live in an environment where food is limiting outside a narrow peak of abundance
131 (Reneerkens et al., 2016; Saalfeld et al. 2019), we expect a positive effect of later hatch dates on chick
132 growth for populations hatching before this food peak, but negative effects for populations hatching
133 after the food peak. We expect that temperature increases may partially mitigate such effects,
134 especially for populations breeding in the coldest conditions. Finally, we explore (3) potential
135 vulnerability of populations to climate warming, by analysing trends in temperature and the trophic
136 mismatch over time.

137 **2. Methods**

138 *2.1 Study populations and sites*

139 We used data on hatch dates and chick growth from six breeding populations of Red Knots, Great
140 Knots and Surfbirds. Great Knots and Surfbirds are monotypic, while Red Knots encompass six
141 subspecies (reviewed in Piersma, 2007), of which four subspecies are included in our study, *C.c.*
142 *islandica*, *C.c. canutus*, *C.c. rogersi* and *C.c. roselaari*. In our analyses we made comparisons between
143 and within subspecies (for Red Knots) and species (for Great Knots and Surfbirds), totalling 6
144 populations. Red Knots, Great Knots and Surfbirds are all medium-sized shorebirds, with adult body
145 masses ranging between 122-154g. Females lay a four-egg clutch, which is incubated by both parents,
146 after which chick care is provided by the male (Red Knot and Great Knot) or by both parents
147 (Surfbird) (Loktionov et al., 2015; Tomkovich, 1995; Tomkovich et al., 1998). Renesting attempts are
148 rare but may occur after nest failure early in the season (Tomkovich, 1991, P. Tomkovich, J. Johnson,
149 pers. comm.). During 21 summer seasons (range 3–10 per population, summing up to a total of 36
150 ‘study years’, Table 1) between 1980 and 2019, these populations were studied at eight study sites
151 with an almost circumpolar distribution (Fig. 2), including sub-Arctic, low-Arctic and high-Arctic
152 sites (Meltofte, 2013). Breeding habitats are characterized by low vegetation, classified as either
153 montane dwarf shrub tundra (Turquoise Lake, Kigluaik Mountains and Upper Anadyr River), coastal

154 plain with dry dwarf shrub and lichen tundra (Meinypilgyno) and Arctic tundra (Knipovich Bay, Cape
155 Sterlegov, Alert, Princess Marie Bay).

156 *2.2 Data collection*

157 *2.2.1 Hatch dates and biometric data of chicks*

158 Between May and August (exact dates varying between study sites) we searched for nests, revisited
159 nests and floated eggs (Liebezeit et al., 2007) to determine hatch dates, and searched for broods.
160 Chicks were banded upon their first capture (either in the nest or later when found as brood). At each
161 capture we measured culmen, tarsus and 10th primary length (to the nearest 0.1 mm), wing length (to
162 the nearest mm) using callipers or a ruler, and body mass (to the nearest 1 g) using a spring or
163 electronic scale. For more details on methods for locating nests and broods, and on determining hatch
164 dates see Supporting information.

165 *2.2.2 Arthropod abundance data*

166 Arthropods are the main prey of shorebirds and their chicks on their breeding grounds (Holmes &
167 Pitelka, 1968). We used abundance of surface-active arthropods as a measure of prey availability for
168 shorebird chicks, which was measured for five of our study populations. Sampling methods differed
169 between sites, but generally comprised a series of pitfall traps placed in the habitat where shorebirds
170 foraged, which were emptied at a regular basis (daily to weekly, see Table S1 for details on methods).
171 Trapped arthropods were counted and identified in the lab at the family level, except at Upper Anadyr
172 River and Turquoise Lake where the total number of trapped arthropods was counted in the field. At
173 all sites, larval stages, Lepidoptera and bumblebees (Apidae) were excluded from the arthropod data as
174 these are not available as prey for chicks (the former dwell underground and the latter two are too
175 large). Collembola were also excluded, as these were not registered at all study sites and are difficult
176 to quantify accurately with the trapping methods used. In addition, the energetic profitability of
177 collembola is low and preliminary data show that they hardly occur in the diet of Red Knot ssp.
178 *canutus* chicks (M.K. Zhemchuzhnikov, pers. comm.). Abundance values were corrected for the
179 number and diameter of pitfall traps, as well as the interval in days between measurements (Table S1).

180 When the interval between trapping dates was more than one day, we corrected the trapping date as
181 the median date of the trapping period. Arthropod abundance was measured at seven of the eight study
182 sites (with the exception of Meinyopilgyno), and not in all years. For our analysis on chick growth in
183 relation to prey availability and relative hatch date, this meant that data were available from 5
184 populations and 13 study years (Table 1). For all other analyses we used all available data for all 6
185 populations and 36 study years (Table 1).

186 *2.2.3 Temperature data*

187 Modelled air temperature at 2 m above surface for all study locations between 1980 and 2019 were
188 downloaded at six-hour resolution, for the period between 1 April and 30 September from the NCEP
189 reanalysis numerical weather model (spatial resolution 1.875° x 1.875° gaussian grid, (Kalnay et al.,
190 1996), using the R package ‘RNCEP’ (Kemp et al., 2012)). The modelled temperature data were
191 evaluated against daily average temperature records collected from a weather station (Vantage Pro2,
192 Davis Instruments) at Knipovich Bay in 2018 and 2019, which resulted in a 0.85 Pearson correlation
193 coefficient (Fig. S1).

194 All data on bird biometrics, arthropod abundance data and modelled air temperature are
195 available online in Lameris et al., (2021a) and Gill Jr. (2022).

196 *2.3 Data preparation*

197 *2.3.1 Estimating age of chicks with unknown hatch date*

198 Nests of our study species are relatively difficult to find (Tomkovich & Loktionov 2020) and many
199 chicks were first encountered when they had already left the nest. To estimate age of such chicks with
200 unknown hatch dates, relationships between age and biometrics for chicks with a known age were
201 used (see Table S2 for sample sizes). As a proxy of age we used either the 10th primary length, or wing
202 length (for Red Knot ssp. *islandica*, and Red Knot ssp. *canutus* at Cape Sterlegov). We fitted logistic
203 growth models predicting 10th primary or wing length from age separately for every population, across

204 different years (Fig. S2, Table S3), and used these to predict age and hatch date of chicks with
205 unknown hatch dates. Complete methods are described in the Supporting information.

206 2.3.2 Modelling chick growth

207 Growth models of body mass increase were fitted on data from individuals with known age together
208 with individuals with predicted age. These models were constructed per population using 3-parameter
209 *von Bertalanffy* growth models as outlined in Tjørve & Tjørve (2017), as these outcompeted logistic
210 and *Gompertz* growth models (Table S4), and 4-parameter *Unified-Richards* models would not
211 converge. As chicks usually have not yet reached adult body mass at fledging (Lindström et al., 2002),
212 we set a fixed upper asymptote A using mean adult body mass (see Appendix S1 for sources of these
213 data). Measurements of chicks younger than 1-day old were excluded, as chicks typically lose body
214 mass during the first day after hatch. As some chicks were captured more than once, we included chick
215 identity as a random effect on growth-rate parameter k . We estimated model parameters (growth-rate k
216 and horizontal placement of inflexion point T) from non-linear least squares, using the package ‘nlme’
217 (Pinheiro et al., 2017) in R 3.4.0 (R Development Core Team, 2020). For each individual chick we
218 calculated a ‘chick condition index’ (Schekkerman et al., 2008), by extracting the residuals from the
219 population-specific *von Bertalanffy* growth models on chick body mass and dividing these residuals by
220 the body mass at that age predicted from the same model.

221 2.3.3 Calculating prey availability and relative hatch date

222 As we were interested in the effect of a trophic mismatch on chick growth, we calculated 1) a direct
223 measure of prey availability for individual chicks, as well as 2) the relative hatch date (relative to the
224 peak in arthropod abundance) for further analyses. To this end, we first modelled dynamics of
225 arthropod abundance over the season using general additive models for every study site and year. We
226 included a thin plate regression spline for the smoothing basis function with day number as predictor
227 variable, and the number of knots ranging between 4 and the maximum number of observations
228 collected throughout the season, from which the best performing model was selected. We determined
229 the peak date in arthropod abundance (per site and year) as the date at which maximum arthropod

230 abundance was found in the general additive models (Fig. 3). We further used the predictions of
231 arthropod abundance from the general additive models as values for daily arthropod abundance, which
232 we log-transformed for further analyses (Schekkerman et al., 2003).

233 1) To calculate prey availability for individual chick observations, we first determined the
234 period of average arthropod abundance which most impacted chick condition, by determining the best
235 performing sliding window using the R package ‘climwin’ (Bailey & van de Pol, 2016). Using a
236 dataset of selected observations of chicks which were at least 15 days old, and a potential window size
237 of 15 days before the day of capture, we found an optimal sliding window of average arthropod
238 abundance between the day of capture and 3 days before (see Supporting information for details on the
239 analysis). We used this time window to calculate average arthropod abundance for individual chick
240 observations.

241 2) We calculated relative hatch date for individual chicks as the difference (in days) between
242 hatch date and arthropod peak date for that site and year. However, the shape and steepness of
243 arthropod peaks, as well as their height varied strongly between sites and years (Fig. 3), and in order to
244 conduct a meaningful analysis across sites and years we needed to correct for this. To this end, relative
245 hatch date was multiplied with a rescaling factor that represents the same loss of arthropod availability
246 compared to the availability at the peak date in all sites and years. We calculated this rescaling factor
247 per individual hatch date, as the difference between the maximum arthropod abundance within the
248 season (as predicted from general additive models) and the mean arthropod abundance during the 20-
249 day period of growth, starting at the individual chick’s hatch date (black line in Fig. 3). This 20-day
250 period was chosen as chicks become volant and independent at about 20 days (Schekkerman et al.,
251 2003). When arthropod abundance data was not available for the entire 20-day period, the average was
252 calculated up to the last date of available arthropod abundance data. We chose this rescaling factor
253 based on the assumptions that I) hatch date relative to the food peak can be a reliable proxy for chick
254 food availability (Ramakers et al., 2019), yet II) when chicks grow up under roughly the same food
255 conditions as around the peak, they will not differ in condition from chicks hatching around the peak.
256 For clarity, we illustrate the rescaled relative hatch dates in an example. Red Knot ssp. *islandica*

257 chicks in Alert experience strong variability in prey dynamics around the peak arthropod date. For
258 example, chicks hatching 5 days after the arthropod peak in 1993 face a much steeper decrease in
259 available prey (relative to the peak) compared to chicks hatching 5 days after the peak in 1999 (Fig. 3).
260 The rescaling factors for these hatch dates and years are 13.6 in 1993 (mean abundance of 5.4
261 compared to peak abundance of 19.0) and 2.4 in 1999 (3.6 compared to 6.0), resulting in a rescaled
262 relative hatch date of 68 ($5 * 13.6$) and 12 ($5 * 2.4$), respectively.

263 We further needed to correct for annual differences in arthropod availability and the height of
264 the arthropod peak, by including these factors in statistical models explaining chick condition (see
265 below). We used the output from the general additive models on arthropod abundance to calculate
266 average arthropod abundance, as the average abundance during the 20-day period of chick growth,
267 starting on the annual average hatch date, and peak height, as the maximum predicted arthropod
268 abundance in the season.

269 *2.3.4 Determining time windows for temperature dependencies*

270 We used modelled temperature data as a predictor variable in analyses on chick condition, as well as
271 to analyse temperature dependencies of hatch dates and arthropod peak dates. As we aimed to compare
272 the impacts of prey availability and temperature on growth, we calculated the average temperature for
273 analyses on chick condition using the same sliding window as found for average arthropod abundance
274 (a 3-day period before the day of capture). As we expected an effect of temperature on condition
275 mostly within populations (with higher condition for chicks growing up under higher temperatures)
276 rather than between populations (where faster growth is associated with lower temperatures, Tjørve et
277 al., 2009), we standardized temperature during growth by subtracting the population-average
278 temperature from individual values.

279 To analyse whether nest initiation dates and arthropod peak dates were impacted by
280 temperatures prior to these dates, we first had to find which period of average temperature most
281 impacted hatch date and arthropod peak date. We analysed this in a sliding-window analysis in the
282 climwin package, using a dataset of annual average nest initiation dates (calculated as 24 days before

283 hatch date, which is the average length of the period required for laying and incubating a typical Red
284 Knot clutch of four eggs; Nettleship., 1974; M.Y. Soloviev, pers. comm.) and a potential window size
285 of 20 days before the site-specific average hatch date. We found an optimal sliding window of average
286 temperature between 16 and 7 days before hatch date (see Supporting information for details on the
287 analysis). This time window was used to calculate average temperature before nest initiation for every
288 site and year. Using the dataset of arthropod peak dates and a potential window size of 20 days before
289 the site-specific average peak date, we found that a base model (with no temperature time window
290 included) performed best, meaning that none of the tested temperature windows significantly impacted
291 arthropod peak dates (see Supporting information for details on the analysis).

292 To analyse trends in temperature during chick growth, we also calculated average temperature
293 for individual chicks during the chick growth period (20 days starting on individual chick hatch date),
294 as well as annual average temperature during the chick growth period (20 days starting on the annual
295 average hatch date at the site).

296 *2.4 Statistical analyses*

297 In the statistical analyses we used linear regression models, linear mixed effects regression models and
298 growth models, constructed in R. We constructed models including all possible combinations of
299 predictor variables of interest and compared model performance using Akaike's information criterion
300 corrected for small sample sizes (AICc, Burnham & Anderson, 2004). The model with the lowest
301 AICc was chosen as our final model. Models within 2 Δ AICc of the final model were considered as
302 competitive as long as these did not contain extra, potentially uninformative, parameters compared to
303 the final model (Arnold, 2010), and in these cases we used averaged parameter estimates of
304 competitive models. Hereafter the specifics for each model used for the different analyses are
305 described.

306 *2.4.1 Variation in growth rate between populations*

307 To analyse how growth rate between populations was impacted by prey availability and temperature,
308 we first modelled population-specific growth rate parameters k in a single *von Bertalanffy* growth

309 model, including data of all populations, with a common parameter value for T but population-specific
310 parameters for k (predicted by including a random effect of population on parameter k). Furthermore, a
311 population-specific parameter A was included as well as chick identity as a random effect on k , nested
312 within population. The performance of this model was compared to a second model that did not
313 include population as a random effect on k . We used linear regression models to analyse how
314 population-specific k -parameters were affected by either population-average temperature during the
315 chick growth period, rescaled relative hatch date, average arthropod abundance or arthropod peak
316 height, which were included as predictor variables in separate models.

317 *2.4.2 Variation in growth rate within populations*

318 We tested the impacts of trophic mismatch and temperature on chick condition by using either our
319 direct measures of prey availability or rescaled relative hatch date. In these analyses we excluded
320 chicks younger than 2 days old, as up to 2 days after hatching chicks mostly survive on their yolk
321 sacks (Starck & Ricklefs, 1998) and variation in condition up to this age is unlikely to be related to
322 prey availability. First, generalized linear mixed effect models were applied to test whether chick
323 condition was affected by prey availability, temperature during the chick growth period, and
324 population. We included interactions of prey availability and temperature with population, and
325 included population-specific year and chick identity as a random intercept. We standardized all
326 predictor variables by dividing them by 2 standard deviations (Gelman, 2008).

327 Hereafter we used generalized linear mixed effect models to test whether chick condition was
328 affected by the predictor variables population, rescaled relative hatch date, rescaled relative hatch date
329 squared (given our prediction of a unimodal response in fitness, Fig. 1a), temperature during the chick
330 growth period, and arthropod peak height or annual average arthropod abundance (as these variables
331 were strongly correlated, Pearson's correlation 0.79, $t = 25.6$, $p < 0.01$). We standardized all predictor
332 variables as explained above. We included interactions of all predictor variables with population, and
333 included chick identity and population-specific year as a random intercept. Model assumptions of
334 linearity, normality, independence and equality of variance were met, based on visual assessment of

335 residual plots, Q-Q plots and correlograms. Variance Inflation Factors ranged between 1.1 and 2.7,
336 suggesting no problematic multicollinearity (Zuur et al., 2010). We analysed whether temperature
337 increases could mitigate effects of trophic mismatch by comparing population-specific Cohen's D
338 effect sizes of rescaled relative hatch date and temperature, for a model including only the predictor
339 variables rescaled relative hatch date, temperature during chick growth, population and the interactions
340 with population.

341 *2.4.3 Correlations between temperature and relative hatch dates*

342 Potential for temperature to mitigate effects of trophic mismatch is only possible when either years or
343 individuals with larger mismatches (due to a later relative hatch date) also experience higher
344 temperatures during chick growth (as suggested in the concept of Fig. 1b). To test this, we used linear
345 regression models to predict temperature during chick growth, with rescaled relative hatch date as
346 predictor variable. Specifically, we used 1) annual average values for rescaled relative hatch date and
347 temperature to test whether mitigation was possible between years, and 2) individual values, year and
348 the interaction with rescaled relative hatch date as additional predictor variable, to test whether
349 mitigation was possible within years.

350 *2.3.4. Change in temperature and relative hatch dates over years*

351 To analyse if climate warming already affects trophic mismatch, we explored whether trophic
352 mismatches and temperatures increased during the overall study period. First, we analysed how
353 modelled annual average temperatures (before nest initiation and during the chick growth period, see
354 above) changed over the period 1990–2019. We analysed time trends using linear regressions models,
355 including year (as continuous variable), study site and their interaction as predictor variables.

356 We then explored potential changes in relative hatch date over time, by analysing how annual
357 variation in hatch dates were affected by temperature. For each site linear regression models were
358 constructed relating hatch date with temperature before nest initiation as predictor variable. Thereafter,
359 we also included study site as predictor variable in all models, as well as interactions between study
360 site and temperature, to assess changes within study sites. We did not test whether annual variation in

361 arthropod peak dates were affected by temperature, as none of the temperature windows had a
362 significant effect (see above). For Red Knot ssp. *roselaari*, *rogersi*, *islandica* at Alert and *canutus* at
363 Knipovich Bay at least four years of data on hatch dates were available, and we tested whether hatch
364 dates advanced over the years in linear regression models including year and study site as predictor
365 variables.

366 **3. Results**

367 *3.1 Variation in growth rate between populations*

368 Growth rate parameters k for Red Knot, Great Knot and Surfbird populations strongly differed from
369 each other (difference between model with one k -parameter and population-specific k -parameters was
370 274 AIC) reflecting large variation in growth rate between populations (Fig. 4, Table 2). Body mass
371 growth rates of chicks were not explained by arthropod peak height, temperature during the chick
372 growth period, rescaled relative hatch date or average arthropod abundance (intercept-only model
373 performed best, Table S6).

374 *3.2 Variation in growth rate within populations*

375 Chick condition increased with prey availability (average $\beta \pm$ standard error: 0.11 ± 0.05 [95%
376 confidence intervals: -0.14; 0.05]; difference between model with and without prey availability 52
377 AIC, Table S7, S8), with slopes differing between populations (difference between model with and
378 without interaction prey availability and population 24 AIC, Table S7, S8). On average, chick
379 condition increased by 3.8% for every additional arthropod per trap per day. Chick condition showed a
380 unimodal response with rescaled relative hatch date (average β rescaled relative hatch date: $0.32 \pm$
381 0.29 [CI: -6.39; 7.01]; average β rescaled relative hatch date squared; -16.26 ± 6.09 [CI: -28.24; -
382 5.65]; Fig. 5, Table 3, 4), with slopes and shapes of this relationship differing between populations
383 (Fig. 5; difference between model with and without interaction rescaled relative hatch date and
384 population 21 AIC ; Table 3, 4). Red Knot ssp. *islandica*, Great Knot and Surfbird showed an initial
385 increase in chick condition (on average 2.7% increase in condition per later day of hatch) followed by
386 a reduction (on average 10.7% decrease in condition per later day of hatch squared). Red Knot ssp.

387 *canutus* and *roselaari* showed an initial reduction in growth (on average 1.2 % reduction in condition
388 per later day of hatch) followed by a slight increase (on average 0.3% increase in condition per later
389 day of squared hatch). Chick condition increased with higher temperature during the chick growth
390 period for some populations (average β : 0.11 ± 0.07 [CI: -0.03; 0.25], difference between model with
391 and without temperature 3.3 AIC, Table 3, 4), with slopes differing between populations (difference
392 between model with and without interaction temperature and population 13.9 AIC). On average, chick
393 condition increased by 1.4% per °C, and notably, the increase in condition with temperature was
394 strongest for Red Knot ssp. *islandica* (6.7% increase in condition per °C; β : 0.37 ± 0.15 [CI: 0.07;
395 0.67], Table 4). In addition, years with higher average arthropod abundance positively affected chicks'
396 condition in Red Knot ssp. *islandica* (1.8% increase in condition per additional arthropod per trap per
397 day), yet negatively in Red Knot ssp. *canutus* and Surfbird (on average 1.6% reduction in condition
398 per additional arthropod per trap per day; difference between model with and without average
399 arthropod abundance 35.1 AIC, difference between model with and without interaction average
400 arthropod abundance and population 32.9 AIC, Table 3, 4).

401 A comparison of population-specific Cohen's D effect sizes for temperature during chick
402 growth and rescaled relative hatch date showed that only for Red Knot ssp. *islandica* the effect size of
403 temperature (0.83) was larger than the negative effect of relative hatch date (-0.32), while for other
404 populations the effect size of temperature (average 0.13) was smaller than the negative effect of
405 relative hatch date (average -0.39).

406 3.3 Correlations between temperature and relative hatch date

407 Between years, we found no trend between temperature and rescaled relative hatch date (intercept-
408 only model performed best, Table S10, Fig. 6a). There were significant year-specific positive trends
409 between temperature and rescaled relative hatch date for most populations, with the exception of Red
410 Knot ssp. *islandica* (Table S10, S11, Fig. 6b).

411 3.4 Changes in temperature and relative hatch date over years

412 Between 1990 and 2019, temperature during the period of chick growth (0.053 ± 0.012 °C/year) and
413 before nest initiation (0.046 ± 0.012 °C/year) increased, with no differences between study sites in
414 rates of increase (Table S12).

415 Hatch dates differed among populations, with populations characterised by earlier hatch dates
416 experiencing higher temperatures before nest initiation (average $\beta \pm$ standard error: -3.62 ± 0.57 [CI: -
417 4.78; -2.47], difference between model including temperature and model without 25.94 AIC, Fig. 6c).
418 Within study sites and between years, hatch dates were not affected by temperatures before nest
419 initiation (model without temperature had less degrees of freedom and 1.82 lower AIC compared to
420 model with, Fig. 6c, Table S13). Hatch dates of Red Knots (all spp.) did not change over time
421 (difference between model with and without year was 3.32 AIC, Table S13, Fig. 6d).

422 **4. Discussion**

423 Using comparisons between and within populations, we found that chick condition was importantly
424 impacted by prey availability, and was highest for chicks hatching early in the season or close to the
425 seasonal food peak. A reduction in chick condition with hatch dates falling later than the food peak
426 signals vulnerability to trophic mismatch in almost all populations. While chick condition generally
427 increased with higher temperatures, temperature increases only mitigated for the effect of later relative
428 hatch date on condition in the population of Red Knot ssp. *islandica* (Table 4), which also experienced
429 the lowest temperatures during chick growth (Fig. 5a).

430 *4.1. Varying responses in chick growth to trophic mismatch between populations*

431 We had predicted the effect of later hatching on chick growth to vary between populations, depending
432 on whether the average chick in a population hatched before or after the food peak. However, hatching
433 before or after the peak did not sufficiently explain differences in response between populations,
434 despite strong variation in response of chick condition to relative hatch date between populations (with
435 unimodal relationships in three out of five populations, and other populations either experiencing a
436 seasonal decline in chick condition or a decline followed by an increase in condition). While chicks of
437 Red Knot ssp. *canutus*, Surfbird, and partially also Red Knot ssp. *roselaari*, were in highest condition

438 when hatching *before* the food peak, chicks of Red Knot ssp. *islandica* and Great Knot were in highest
439 condition when hatching *shortly after* the food peak.

440 Given that we also find a positive effect of prey availability on chick condition, the moment in
441 the season when condition peaks likely depends on the extent to which food is limiting growth before
442 or after the food peak. For example, chicks of Red Knot ssp. *canutus* experience a seasonal decline in
443 condition that sets in at hatch dates before the food peak, suggesting food to be limiting growth for all
444 but the earliest hatching chicks. While we do not know at which age chicks would be most sensitive to
445 variations in food availability, energetic costs and therefore required energy intake for chicks increase
446 with age (Schekkerman et al., 2003; Williams et al., 2007), which makes it profitable to hatch before
447 the food peak (Saalfeld et al., 2019; Schekkerman et al., 2003). On the other hand, chicks of Red Knot
448 ssp. *islandica*, which showed a distinct peak in condition shortly after the food peak, likely faced food
449 limitations when hatching before as well as after the food peak. Such food limitations prior to the food
450 peak also applied to Red Knot ssp. *roselaari*, which hatched relatively far in front of the food peak.

451 These population-specific responses of chick condition to later hatch dates signify the
452 importance of periods with adequate food availability, when availability exceeds some minimum
453 threshold that is crucial for rapid chick growth (Reneerkens et al., 2016; Saalfeld et al., 2019; Vatka et
454 al., 2014). The length of this period is likely to be a key determinant in fitness response to trophic
455 mismatches. For such a measure, one would ideally use data on required energy intake (Schekkerman
456 et al., 2003) to estimate a threshold when food would be limiting growth, and calculate a ‘peak width’
457 from arthropod data available for the entire summer season (e.g. Reneerkens et al., 2016; Visser et al.
458 2005). This would also help to better capture multiple peaks in resource availability throughout the
459 season rather than the oversimplification of determining a single peak. However, this could not be
460 done for the present data set, because most site-year combinations did not cover the entire summer.

461 Our study faces other limitations which may reduce the strength of the analysis. First, while
462 we have assumed that chicks feed on all available arthropods, they might be more specific in their diet.
463 If chicks are specifically selecting for certain prey, this will have an important impact on the relevant

464 peak in prey availability, and peak date of all arthropods may be an inappropriate yardstick (Visser &
465 Both, 2005). Incorporating specific knowledge on shorebird diet in these analyses via e.g., DNA
466 analyses of feces (Wirta et al., 2015), is an important (next) step in studying trophic mismatches
467 (Cholewa & Wesolowski, 2011; Samplonius et al., 2016; 2021; Zhemchuzhnikov et al. 2021). Another
468 limitation of our study is the use of arthropod numbers rather than biomass (as this data was not
469 available for all populations), and the relatively low number of years with data on arthropods. These
470 limitations may also explain the surprising result that for Surfbird and Red Knot ssp. *canutus* we found
471 a negative relationship between annual average arthropod abundance and chick condition. With only 3
472 years of data available for these populations, this effect may well be explain by other factors varying
473 between years. Moreover, for Red Knot ssp. *roselaari* and Great Knot, we have only one year of
474 combined bird and arthropod data, and population and study site are confounding factors for most
475 populations. Also, large variation exists in the years of data collection, with data from some
476 populations only available for the 1990's, while data for other populations is only available from the
477 last decade. This may limit the potential for comparative analyses. It is also noteworthy that our
478 method of estimating age is only valid under the assumption that structural growth is unregulated by
479 environmental conditions. Although we found strong correlations between known age and 10th primary
480 / wing length, environmental conditions have been shown to also impact structural growth (Lloyd and
481 Martin 2004; Auer and Martin 2017). However, even if chicks with smaller structural sizes are
482 incorrectly estimated to be of younger age, this would lead to an underestimation of the effects of
483 temperature and relative hatch date of chick condition index due to smaller residual estimates.

484 *4.2. Little potential for temperature mitigating negative effects of mismatches*

485 We found a positive effect of temperature on chick condition for some populations, with the strongest
486 effect found for Red Knot ssp. *islandica*, yet little effect for other populations. In general, effects of
487 temperature on avian growth appear to be variable (Sauve et al., 2021). When considering Arctic-
488 nesting shorebirds, some studies found positive effects of temperature on growth (McKinnon et al.,
489 2013; Schekkerman et al., 1998, 2003; Tjørve et al., 2007) while other studies did not (Machín et al.,
490 2018; Saalfeld et al., 2019) or found an effect in one year but not in the next due to annual differences

491 in observed temperature ranges (Tulp 2007). Physiologically, a positive effect of temperature would
492 be expected, given that temperatures at times fall below the thermoneutral zone (below the lower
493 critical temperature, which is 19.9 °C for adult Red Knots; Wiersma & Piersma, 1994, but probably
494 higher for chicks; Bakken et al. 2002; Visser & Ricklefs 1993; Visser 1998). Chicks require more
495 energy when facing low temperatures (Bakken et al., 2002), but may be protected from such
496 conditions by the use of microhabitats with protective cover (Wiersma & Piersma, 1994) or by being
497 brooded by their parents (Krijgsveld et al., 2003; Schekkerman et al., 2003).

498 Chicks of Red Knot ssp. *islandica* grow up under the coldest conditions relative to other
499 populations in this study (1.27° C compared to 10.01° C for all other populations). Under such
500 conditions, low temperatures probably become a limiting factor for growth, which explains the strong
501 positive effect of temperature on chick condition in this population. In fact, we find that in this
502 population the effect of temperature on chick condition is larger than that of rescaled relative hatch
503 date, meaning that increasing temperatures may compensate for the effect of a mismatch. However,
504 temperatures appear to be rather stable throughout the growing period of chicks, which means that
505 there is little potential for a mitigating effect of temperatures within the season, as previously
506 suggested (McKinnon et al., 2013). Instead, it appears that for chicks of Red Knot ssp. *islandica*
507 mitigation can take place between years, as in years in which the trophic mismatch is larger,
508 temperatures during growth are also higher (Fig. 7, Pearson's correlation between temperature and
509 rescaled relative hatch = 0.93, $p = 0.07$). While for most populations, food availability will be a more
510 important determinant of energetics and growth (Schekkerman & Visser, 2001; Schekkerman et al.,
511 2003; Senner et al., 2017) as well as survival (Saalfeld et al. 2021), temperatures appear to have an
512 important effect on condition for chicks growing up in the coldest conditions. This means that
513 temperatures may compensate for growth reductions induced by a trophic mismatch only under
514 specific conditions (see also McKinnon et al., 2013), but it is unlikely that this applies as a general
515 rule.

516 *4.3. Vulnerability to trophic mismatch in a warming climate*

517 While temperature as a mitigating factor may be only relevant for populations growing up in what now
518 are extremely cold conditions, and may therefore become less relevant in a world that warms up,
519 trophic mismatches will potentially increase in frequency and extent (Renner & Zohner, 2018). This is
520 because organisms at higher trophic levels appear to generally respond slower to climatic changes than
521 their prey at lower trophic levels (Both et al., 2009; Thackeray et al., 2010). Whereas we did find that
522 populations living in warmer environments have earlier hatching dates, we found no response of hatch
523 dates to temperatures within populations, nor did we find a change in hatch dates over the years for
524 Red Knots (*ssp. islandica, canutus, rogersi* and *roselaari*). It is noteworthy, however, that hatch dates
525 in this study were based solely on successful nests, which may create a bias towards later nests
526 (Verhoeven et al., 2020) if early nests are more prone to predation (Reneerkens et al., 2016).

527 On the one hand, a lack of change in hatch dates over longer time periods could reflect little
528 change in arthropod peak dates. We find that temperatures alone cannot predict arthropod peak dates,
529 which aligns with the idea that phenology of arthropod emergence as well as activity is caused by a
530 combination of interacting climatic variables (Koltz et al., 2018; Shaftel et al., 2021; Tulp &
531 Schekkerman, 2008) and therefore difficult to predict. Moreover, the importance of climatic variables
532 in determining phenology may differ between invertebrate taxa (Koltz et al., 2018). Phenological
533 advancements in arthropod emergence have nevertheless been shown in some time series (Høye et al.,
534 2007; Rakhimberdiev et al., 2018, but see Møller et al. 2021) and predicted from climatic
535 dependencies (Shaftel et al., 2021; Tulp & Schekkerman, 2008). How such advancements impact food
536 available for shorebird chicks will also depend on climate-induced changes in arthropod community
537 composition (Høye et al., 2021; Koltz et al., 2018), body size (Tseng et al., 2018) activity (Høye &
538 Forchhammer, 2008), and variation in abundance outside of the peak (Machín et al., 2018; Saalfeld et
539 al., 2019). Therefore, whether the occurrence of trophic mismatches is increasing for Arctic-nesting
540 shorebirds is currently unclear.

541 On the other hand, even with advancing arthropod peaks, a lack of response in timing of
542 reproduction is not unexpected and is found in many migratory bird species (Knudsen et al., 2011;
543 Samplonius et al., 2018), including many Arctic-nesting bird species (Lameris et al., 2019; Møller et

544 al. 2021; Reneerkens et al., 2016; Saalfeld & Lanctot, 2017; but see Rakhimberdiev et al., 2018). This
545 may be explained by the fact that migrants are unable to forecast changing conditions on the breeding
546 grounds from their distant wintering grounds (Kölzsch et al., 2015; Piersma et al. 1990; Winkler et al.,
547 2014). Also, birds may be too time-constrained to advance their timing of migration (Lameris et al.,
548 2018; 2021b; Lindström et al. 2019, Rakhimberdiev et al., 2018), are forced to delay egg-laying in
549 years with high snow cover (Schmidt et al., 2019) or face larger nest predation danger when initiating
550 nests early (Borgmann et al., 2013; Byrkjedal 1980; Meltofte et al. 2021; Reneerkens et al., 2016).

551 Although it remains unclear if trophic mismatches have population-level consequences
552 (Franks et al., 2017; Miller-Rushing et al., 2010), reductions in growth rate, as we find in our study,
553 may lead to reductions in chick survival (Sedinger et al., 1995), and lower chick survival has also been
554 associated with trophic mismatch (Lameris et al. 2018; Saalfeld et al. 2021). In addition, growth
555 reductions may carry over to later life stages via smaller biometrics impacting foraging efficiency and
556 survival in wintering areas (van Gils et al., 2016), or via reductions in survival and longevity as a
557 consequence of compensatory growth with accompanying accumulation of cellular damage (Mangel &
558 Munch, 2005). We find also strong population differences in growth reduction with later hatch dates,
559 which are likely explained by the moment when arthropod abundance becomes a limiting factor for
560 growth. Therefore, the shape of seasonal arthropod dynamics appears to be an essential determinant
561 explaining variation in the vulnerability of populations to trophic mismatch, at least for Arctic-
562 breeding shorebirds. Moreover, we find that mismatch-induced growth reductions are only
563 compensated for by temperature increases for chicks growing up under extremely low temperatures. In
564 most areas the potential benefit of increased temperature is dwarfed by reductions in food due to
565 mismatches. Together, this implies that it will be mostly knowledge on annual and seasonal
566 fluctuations in food availability that will aid in assessing the vulnerability of populations to trophic
567 mismatch.

568 **Acknowledgements**

569 This work was supported by a grant from the Netherlands Polar Programme, which is part of the
570 Netherlands Organization for Scientific Research (ALWPP.2016.044 awarded to J.A. van Gils). We
571 thank all who assisted in nest searches and capturing shorebird chicks during expeditions to Alert
572 (Clare Hodgetts, Nick Davidson and other field participants), Cape Sterlegov (Petra de Goeij, Joop
573 Jukema, Jan van de Kam), Knipovich Bay (Viktor Golovniuk, Anastasia Popovkina, Maria Sukhova,
574 Elena Lappo), Upper Anadyr River (Dmitry Te, Dmitry Shitikov), Meinypilgyno (Egor Loktionov,
575 Tong Mu and many others), Kigluaik Mountains (Nick Hajdukovich, Laura McDuffie, Callie
576 Gesmundo, and many others) and Turquoise Lake (Alan Bennett, Colleen Handel). At Alert, special
577 thanks go to military personnel at Canadian Forces Station Alert and the Environment Canada
578 Weather Station for logistical support. We thank the Polar Continental Shelf Project (Government of
579 Canada) and Environment Canada for support at Princess Marie Bay and Alert, and members of the
580 Joint Services Expeditions to Princess Marie Bay and Borup Fjord, Ellesmere Island, for their
581 contributions. The 1994 effort at Cape Sterlegov was made possible by gifts from 80 private donors
582 and further funding from the Netherlands Organization for Scientific Research, Netherlands Ministry
583 of LNV, Stichting Plancius, and received help from Gerard Boere, the Great Arctic Reserve,
584 University of Lund, and the Institute of Evolutionary Morphology and Ecology of the Russian
585 Academy of Sciences. Studies in Meinypilgyno were conducted during expeditions by BirdsRussia.
586 We thank Jeroen Reneerkens, Tom Versluijs, Anieke van Leeuwen, Roos Kentie at the department of
587 Coastal Systems of the Royal NIOZ and Chiel Boom at the Netherlands Institute for Ecology for
588 comments on the analyses provided in this manuscript. We thank Liam Bailey for help with analyses
589 using the r-package climwin. Finally, we thank two anonymous reviewers for providing guidance in
590 improving the manuscript.

591 Work on Surfbirds was conducted in accordance with the U.S. Geological Survey Alaska Science
592 Center Animal Care and Use Committee protocols for the “Pacific Shorebird Migration Project.” Any
593 use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement
594 by the U.S. Government.

595 **Data availability statement**

596 The data that support the findings of this study are openly available in Mendeley Data at
597 <http://doi.org/10.17632/3sfrd695hf.3> and from the U.S. Geological Survey at
598 <https://doi.org/10.5066/P9VDI8RZ>.

599 **References**

- 600 Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike ' s information
601 criterion. *Journal of Wildlife Management*, *74*, 1175–1178.
- 602 Bailey, L. D., & van de Pol, M. (2016). Climwin: An R Toolbox for Climate Window Analysis. *PLoS*
603 *ONE*, *11*, e0167980
- 604 Bakken, G. S., Williams, J. B., & Ricklefs, R. E. (2002). Metabolic response to wind of downy chicks
605 of Arctic-breeding shorebirds (Scolopacidae). *Journal of Experimental Biology*, *205*, 3435–3443.
- 606 Bartoń, K. (2019). *MuMIn: multi-model inference*. R package (p. Online). [http://cran.r-](http://cran.r-project.org/web/packages/MuMIn/index.html)
607 [project.org/web/packages/MuMIn/index.html](http://cran.r-project.org/web/packages/MuMIn/index.html)
- 608 Borgmann, K. L., Conway, C. J., & Morrison, M. L. (2013). Breeding phenology of birds:
609 mechanisms underlying seasonal declines in the risk of nest predation. *PLoS ONE*, *8*, e65909.
- 610 Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change
611 and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal*
612 *of Animal Ecology*, *78*, 73–83.
- 613 Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F. W., Brown,
614 R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V., Walsh, J., Overland, J., Wang, M., Corell,
615 R. W., Meier, W. N., Wouters, B., Mernild, S., Mard, J., Pawlak, J., & Olsen, M. S. (2019). Key
616 indicators of Arctic climate change : 1971 – 2017. *Environmental Research Letters*, *14*, 045010.
- 617 Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in
618 model selection. *Sociological Methods and Research*, *33*, 261–304.
- 619 Byrkjedal, I. (1980). Nest predation in relation to snow-cover: a possible factor influencing the start of

620 breeding in shorebirds. *Ornis Scandinavica*, 11, 249-252.

621 Cholewa M. & Wesolowski T. (2011). Nestling food of European hole-nesting passerines: do we
622 know enough to test the adaptive hypotheses on breeding seasons? *Acta Ornithologica*, 46, 105–
623 116.

624 Corkery, C. A., Nol, E., & Mckinnon, L. (2019). No effects of asynchrony between hatching and peak
625 food availability on chick growth in Semipalmated Plovers (*Charadrius semipalmatus*) near
626 Churchill, Manitoba. *Polar Biology*, 0123456789.

627 Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of
628 young in an Arctic herbivore. *Global Change Biology*, 21, 4364–4376.

629 Drent, R. H. (2006). The timing of birds ' breeding seasons : the Perrins hypothesis revisited especially
630 for migrants. *Ardea*, 94, 305–322.

631 Drent, R.H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea*,
632 68, 225-252.

633 Franks, S. E., Pearce-Higgins, J. W., Atkinson, S., Bell, J. R., Botham, M. S., Brereton, T. M.,
634 Harrington, R., & Leech, D. I. (2017). The sensitivity of breeding songbirds to changes in
635 seasonal timing is linked to population change but cannot be directly attributed to the effects of
636 trophic asynchrony on productivity. *Global Change Biology*, 24, 957–971.

637 Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in*
638 *medicine*, 27, 2865-73.

639 Gibson, R., & Baker, A. (2012). Molecular phylogenetics and evolution multiple gene sequences
640 resolve phylogenetic relationships in the shorebird suborder Scolopaci (Aves : Charadriiformes).
641 *Molecular Phylogenetics and Evolution*, 64, 66–72.

642 Gill, R.E., Jr. (2022) Hatch dates and chick growth data from surfbirds (*Calidris virgata*), Turquoise
643 Lake, Alaska, 1997-1999: *U.S. Geological Survey data release*,

644 <https://doi.org/10.5066/P9VDI8RZ>

645 van Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., de Fouw, J., Rakhimberdiev, E.,
646 Soloviev, M., Piersma, T., & Klaassen, M. (2016). Body shrinkage due to Arctic warming
647 reduces red knot fitness in tropical wintering range. *Science*, 352, 819–821.

648 Holmes, R. T., & Pitelka, F. A. (1968). Food Overlap Among Coexisting Sandpipers on Northern
649 Alaskan Tundra. *Systematic Zoology*, 17, 305–318.

650 Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid
651 advancement of spring in the High Arctic. *Current Biology*, 17, 449–451.

652 Høye, T. T., & Forchhammer, M. C. (2008). The influence of weather conditions on the activity of
653 high-arctic arthropods inferred from long-term observations. *BMC Ecology*, 8, 1–7.

654 Høye, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J., Schmidt, N.M.(2021).
655 Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic
656 arthropods. *Proceedings of the National Academy of Sciences of the United States of America*,
657 118, e2002557117.

658 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S.,
659 White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.
660 C., Ropelewski, C., Wang, J., Leetmaa, A., ... Joseph, D. (1996). The NCEP/NCAR 40-year
661 reanalysis project. *Bulletin of the American Meteorological Society* 77, 437–471.

662 Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., & Bouten, W. (2012). RNCEP: Global
663 weather and climate data at your fingertips. *Methods in Ecology and Evolution*, 3, 65–70.

664 Kersten, M., & Piersma, T. (1987). High levels of energy expenditure in shorebirds: metabolic
665 adaptations to an energetically expensive way of life. *Ardea*, 75, 175–187.

666 Kharouba, H. M., & Wolkovich, E. M. (2020). Disconnects between ecological theory and data in
667 phenological mismatch research. *Nature Climate Change*, 10, 406–415.

668 Klaassen, M., Bech, C., Masman, D., & Slagsvold, G. (1989). Growth and energetics of Arctic tern
669 chicks (*Sterna paradisaea*). *Auk*, *106*, 240–248.

670 Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A.,
671 Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E.,
672 Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging
673 claims in the study of migratory birds and climate change. *Biological Reviews*, *86*, 928–946.

674 Koltz, A. M., Schmidt, N. M., & Høye, T. T. (2018). Differential arthropod responses to warming are
675 altering the structure of arctic communities. *Royal Society Open Science*, *5*, 171503.

676 Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K.-M., van der Jeugd, H. P., & Nolet,
677 B. a. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology
678 along different migration routes of an avian herbivore. *Journal of Animal Ecology*, *84*, 272–283.

679 Krijgsveld, K. L., Reneerkens, J. W., McNett, G. D., & Ricklefs, R. E. (2003). Time budgets and body
680 temperatures of American golden-plover chicks in relation to ambient temperature. *Condor*, *105*,
681 268–278.

682 Kwon, E., Weiser, E. L., Lanctot, R. B., Brown, S. C., Gates, H. R., Gilchrist, G., Lank, D. B.,
683 Liebezeit, J. R., Mckinnon, L., Nol, E., Payer, D. C., Rausch, J., Rinella, D. J., Saalfeld, S. T.,
684 Senner, N. R., Smith, P. A., Ward, D., Wisseman, R. W., & Sandercock, B. K. (2019).
685 Geographic variation in the intensity of warming and phenological mismatch between Arctic
686 shorebirds and invertebrates. *Ecological Monographs*, *89*, 1–20.

687 Lameris, T.K., Tomkovich, P.S., Johnson, J.A., Morrison, R.I.G., Tulp, I., Lisovski, S., DeCicco, L.,
688 Dementyev, M., Gill Jr., R.E., ten Horn, J., Piersma, T., Pohlen, Z., Schekkerman, H., Soloviev,
689 M., Syroechkovsky, E.E., Zhemchuzhnikov, M.K. & van Gils, J.A. (2021a). Data from:
690 Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely
691 mitigated by increasing temperatures. *Mendeley Data*, *V2*, doi: 10.17632/3sfrd695hf.3

692 Lameris, T. K., Dokter, A. M., van der Jeugd, H. P., Bouten, W., Koster, J., Sand, S. H. H.,

693 Westerduin, C., & Nolet, B. A. (2021b). Nocturnal foraging lifts time constraints in winter for
694 migratory geese but hardly speeds up fueling. *Behavioral Ecology*, *32*, 539–552.

695 Lameris, T. K., Jong, M. E. De, Boom, M. P., Jeugd, H. P. Van Der, & Litvin, K. E. (2019). Climate
696 warming may affect the optimal timing of reproduction for migratory geese differently in the low
697 and high Arctic. *Oecologia*, *191*, 1003–1014.

698 Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin,
699 K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but
700 still suffer from a phenological mismatch. *Current Biology*, *28*, 2467–2473.

701 Lameris, T. K., Jochems, F., van der Graaf, A. J., Andersson, M., Limpens, J., & Nolet, B. A. (2017).
702 Forage plants of an Arctic-nesting herbivore show larger warming response in breeding than
703 wintering grounds, potentially disrupting migration phenology. *Ecology and Evolution*, *7*, 2652–
704 2660.

705 Liebezeit, J. R., Smith, P. A., Lanctot, R. B., Schekkerman, H., Kendall, S. J., Tracy, D. M.,
706 Rodrigues, R. J., Meltofte, H., Robinson, J. A., Gratto-Trevor, C., McCaffery, B. J., Morse, J., &
707 Zack, S. W. (2007). Assessing the development of shorebird eggs using the flotation method:
708 species-specific and generalized regression models. *Condor*, *109*, 32–47.

709 Lindholm, A., Gauthier, G., & Desrochers, A. (1994). Effects of hatch date and food supply on gosling
710 growth in Arctic-nesting greater snow geese. *Condor*, *96*, 898–908.

711 Lindström, Å., Klaassen, M., Piersma, T., Holmgren, N., & Wennerberg, L. (2002). Fuel stores of
712 juvenile waders on autumn migration in high arctic Canada. *Ardea*, *90*, 93–101.

713 Lindström, Å., Alerstam, T., & Hedenström, A. (2019). Faster fuelling is the key to faster migration.
714 *Nature Climate Change*, *9*, 288–289.

715 Loktionov, E. Y., Tomkovich, P. S., & Porter, R. R. (2015). Study of incubation, chick rearing and
716 breeding phenology of Red Knots. *Wader Study*, *122*, 142–152.

- 717 Loonstra, A. H. J., Verhoeven, M. A., & Piersma, T. (2018). Sex-specific growth in chicks of the
718 sexually dimorphic Black-tailed Godwit. *Ibis*, *160*, 89–100.
- 719 Machín, P., Fernández-Elipe, J., & Klaassen, R. H. G. (2018). The relative importance of food
720 abundance and weather on the growth of a sub-arctic shorebird chick. *Behavioral Ecology and*
721 *Sociobiology*, *72*.
- 722 Mangel, M., & Munch, S. B. (2005). A life-history perspective on short- and long-term consequences
723 of compensatory growth. *American Naturalist*, *166*, E155-E176.
- 724 McKinnon, L., Nol, E., & Juillet, C. (2013). Arctic-nesting birds find physiological relief in the face of
725 trophic constraints. *Scientific Reports*, *3*, 1-6.
- 726 Meltofte, H. (2013). What is the Arctic and who are Arctic waders? *Wader Study*, *124*, 169–171.
- 727 Meltofte, H., Hansen, J., & Rigét, F. (2021). Trends in breeding performance in wader populations at
728 Zackenberg, high Arctic Greenland, in relation to environmental drivers 1996–2018. *Polar*
729 *Biology*, In press.
- 730 Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological
731 mismatches on demography. *Philosophical Transactions of the Royal Society B*, *365*, 3177–
732 3186.
- 733 Nettleship, D. (1974). The Breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island,
734 N.W.T. *Polarforschung*, *44*, 8–26.
- 735 Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E.,
736 Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green,
737 R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014). Mechanisms
738 underpinning climatic impacts on natural populations: Altered species interactions are more
739 important than direct effects. *Global Change Biology*, *20*, 2221–2229.
- 740 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Eispack, Heisterkamp, S., & Van Willigen, B. (2017).

741 Linear and Nonlinear Mixed Effects Models Description. R Package, version 3., 1–336.

742 Perrins, C. M. (1970). The timing of birds' breeding seasons. *Ibis*, *112*, 242–255.

743 Piersma, T., Klaassen, M., Bruggemann, J.H., Blomert, A.-M., Gueye, A., Ntiamoa-Baidu, Y., & van
744 Brederode, N.E. (1990). Seasonal timing of the spring departure of waders from the Banc
745 d'Arguin, Mauritania. *Ardea*, *78*, 123-134.

746 Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of
747 shorebirds worldwide. *Journal of Ornithology*, *148*, S45–S59.

748 Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic
749 herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B*, *363*,
750 2369–2375.

751 Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and warming
752 with latitude over the past century. *Scientific Reports*, *8*, 1–8.

753 R Development Core Team. (2020). *R: A language and environment for statistical computing*. (p.). R
754 foundation for Statistical Computing, <http://cran.r-project.org/bin/windows/base/>.

755 Rakhimberdiev, E., Duijns, S., Camphuysen, C. J., VRS Castricum, Dekinga, A., Dekker, R.,
756 Gavrilov, A., ten Horn, J., Jukema, J., Karagicheva, J., Saveliev, A., Soloviec, M., Tibbitts, T. L.,
757 van Gils, J. A., & Piersma, T. (2018). Fuelling conditions at staging sites can mitigate Arctic
758 warming effects in a migratory bird. *Nature Communications*, *9*, 4263.

759 Ramakers, J. J. C., Gienapp, P., & Visser, M. E. (2019). Comparing two measures of phenological
760 synchrony in a predator–prey interaction: Simpler works better. *Journal of Animal Ecology*, *89*,
761 745-756.

762 Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual
763 fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, *82*,
764 131–144.

765 Reneerkens, J., Schmidt, N. M., Gilg, O., Hansen, J., Hansen, L. H., Moreau, J., & Piersma, T. (2016).
766 Effects of food abundance and early clutch predation on reproductive timing in a high Arctic
767 shorebird exposed to advancements in arthropod abundance. *Ecology and Evolution*, 6, 7375–
768 7386.

769 Renner, S. S., & Zohner, C. M. (2018). Climate Change and Phenological Mismatch in Trophic
770 Interactions Among Plants, Insects, and Vertebrates. *Annual Review of Ecology, Evolution, and*
771 *Systematics*, 49,

772 Saalfeld, S. T., & Lanctot, R. B. (2017). Multispecies comparisons of adaptability to climate change:
773 A role for life-history characteristics? *Ecology and Evolution*, 7, 10492–10502.

774 Saalfeld, S. T., Mcewen, D. C., Kesler, D. C., Butler, M. G., Cunningham, J. A., Doll, A. C., English,
775 W. B., Gerik, D. E., Grond, K., Herzog, P., Hill, B. L., Lagassé, B. J., & Lanctot, R. B. (2019).
776 Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable
777 weather conditions on food availability and chick growth. *Ecology & Evolution*, 9, 6693–6707.

778 Saalfeld, S. T., Hill, B. L., Hunter, C. M., Frost, C. J., & Lanctot, R. B. (2021). Warming Arctic
779 summers unlikely to increase productivity of shorebirds through reneating. *Scientific Reports*, 11,
780 15277.

781 Samplonius, J. M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S. J., Assmann, J. J., Burgess,
782 M. D., Johansson, J., Macphie, K. H., Pearce-Higgins, J. W., Simmonds, E. G., Varpe, Ø., Weir,
783 J. C., Childs, D. Z., Cole, E. F., Daunt, F., Hart, T., Lewis, O. T., Pettorelli, N., ... Phillimore, A.
784 B. (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony
785 and its impacts. *Nature Ecology and Evolution*, 5, 155–164.

786 Samplonius, J. M., Bartošová, L., Burgess, M. D., Bushuev, A. V., Eeva, T., Ivankina, E. V., Kerimov,
787 A. B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M.
788 E., Zang, H., & Both, C. (2018). Phenological sensitivity to climate change is higher in resident
789 than in migrant bird populations among European cavity breeders. *Global Change Biology*, 24,

- 790 3780–3790.
- 791 Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and
792 ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal*
793 *Ecology*, *85*, 1255–1264.
- 794 Sauve, D., Friesen, V. L., & Charmantier, A. (2021). The Effects of Weather on Avian Growth and
795 Implications for Adaptation to Climate Change. *Frontiers in Ecology and Evolution*, *9*, 1–20.
- 796 Schekkerman, H, van Roomen, M. W. J., & Underhill, L. G. (1998). Growth , behaviour of broods and
797 weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*.
798 *Ardea*, *86*, 153-168.
- 799 Schekkerman, H., Tulp, I., Piersma, T., & Visser, G. H. (2003). Mechanisms promoting higher growth
800 rate in arctic than in temperate shorebirds. *Oecologia*, *134*, 332–342.
- 801 Schekkerman, H., & Visser, G. H. (2001). Prefledging energy requirements in shorebirds: energetic
802 implications of self-feeding precocial development. *Auk*, *118*, 944–957.
- 803 Schekkerman, H., Teunissen, W., Oosterveld, E. (2008). The effect of ‘mosaic management’ on the
804 demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology*, *45*,
805 1067–1075.
- 806 Schmidt, N. M., Reneerkens, J., Christensen, J. H., Olesen, M., & Roslin, T. (2019). An ecosystem-
807 wide reproductive failure with more snow in the Arctic. *PLoS Biology*, *17*, e3000392.
- 808 Sedinger, J. S., Flint, P. L., & Lindberg, M. S. (1995). Environmental influence on life-history traits:
809 Growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology*, *76*, 2404–2414.
- 810 Senner, N. R., Stager, M., & Sandercock, B. K. (2017). Ecological mismatches are moderated by local
811 conditions for two populations of a long- distance migratory bird. *Oikos*, *126*, 61–72.
- 812 Serreze, M. C., & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research

813 synthesis. *Global and Planetary Change*, 77, 85–96.

814 Shaftel, R., Rinella, D. J., Kwon, E., Brown, S. C., Gates, H. R., Kendall, S., Lank, D. B., Liebezeit, J.
815 R., Payer, D. C., Rausch, J., & Saalfeld, S. T. (2021). Predictors of invertebrate biomass and rate
816 of advancement of invertebrate phenology across eight sites in the North American Arctic. *Polar*
817 *Biology*, 44, 237-257.

818 Starck, J. M., & Ricklefs, R. E. (eds.) (1998). *Avian growth and development*. Oxford University
819 Press.

820 Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P.,
821 Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J.,
822 Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S.
823 (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241–245.

824 Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S.,
825 Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M.,
826 Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S.
827 (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and
828 terrestrial environments. *Global Change Biology*, 16, 3304–3313.

829 Thomas, G. H., Wills, M. A., & Székely, T. (2004). A supertree approach to shorebird phylogeny.
830 *BMC Evolutionary Biology*, 4, 1–18.

831 Tjørve, K. M. C., García-Peña, G. E., & Székely, T. (2009). Chick growth rates in Charadriiformes:
832 Comparative analyses of breeding climate, development mode and parental care. *Journal of*
833 *Avian Biology*, 40, 553–558.

834 Tjørve, K. M. C., Schekkerman, H., Tulp, I., Underhill, L. G., De Leeuw, J. J., & Visser, G. H. (2007).
835 Growth and energetics of a small shorebird species in a cold environment: The little stint
836 *Calidris minuta* on the Taimyr Peninsula, Siberia. *Journal of Avian Biology*, 38, 552–563.

837 Tjørve, K. M. C., & Tjørve, E. (2017). Modelling avian growth with the Unified-Richards: as

838 exemplified by wader-chick growth. *Journal of Avian Biology*, 48, 770–784.

839 Tomkovich, P. S. (1991). Breeding biology of the Great Knots, *Calidris tenuirostris*. *Bulletin of*
840 *Moscow Society of Naturalists*, 106, 13–22.

841 Tomkovich, P. S. (1995). Second report on research on the Great Knot *Calidris tenuirostris* on the
842 breeding grounds. *Wader Study Group Bull.*, 78, 50–52.

843 Tomkovich, P. S., Gill, R. E., & Dementiev, M. N. (1998). Surfbird in its non-surfing habitats. *Dutch*
844 *Birding*, 20, 233–237.

845 Tomkovich P.S., Loktionov, E.Y. (2020) An experience of search for nests of “difficult” waders: the
846 red knot *calidris canutus* as an example. *Ornithologia*, 44, 87–92

847 Tseng, M., Kaur, K. M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., Toor,
848 H. S., & Fograscher, K. (2018). Decreases in beetle body size linked to climate change and
849 warming temperatures. *Journal of Animal Ecology*, 87, 647–659.

850 Tulp, I. (2007) The arctic pulse: Timing of breeding in long-distance migrant shorebirds. PhD-thesis,
851 University of Groningen, 259 pp.

852 Tulp, I., & Schekkerman, H. (2008). Has prey availability for arctic birds advanced with climate
853 change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation.
854 *Arctic*, 61, 48–60.

855 Vatka, E., Orell, M., & Rytönen, S. (2016). The relevance of food peak architecture in trophic
856 interactions. *Global Change Biology*, 22, 1585–1594.

857 Vatka, E., Rytönen, S., & Orell, M. (2014). Does the temporal mismatch hypothesis match in boreal
858 populations? *Oecologia*, 176, 595–605.

859 Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Macias, P., Kaspersma, W., Hooijmeijer, J. C.
860 E. W., van der Velde, E., Both, C., Senner, N. R., & Piersma, T. (2020). Geolocators lead to
861 better measures of timing and reneating in black-tailed godwits and reveal the bias of traditional

- 862 observational methods. *Journal of Avian Biology*, 51, 1–12.
- 863 Visser, G.H. (1998). Development of temperature regulation. Pp 177-156 in: Starck M. & R. Ricklefs,
864 Avian growth and development. Oxford University Press, New York.
- 865 Visser, G.H., & Ricklefs, R. E. (1993). Development of temperature regulation in shorebirds.
866 *Physiological Zoology*, 66, 771–792.
- 867 Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need for a
868 yardstick. *Proceedings of the Royal Society B*, 272, 2561–2569.
- 869 Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global climate change leads to mistimed avian
870 reproduction. *Advances in Ecological Research*, 35, 89–110.
- 871 Visser, M.E., Holleman, L.J.M, Gienapp, P. (2005). Shifts in caterpillar biomass phenology due to
872 climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147,
873 164-172.
- 874 Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological
875 mismatches. *Nature Ecology & Evolution*, 12, 879-885.
- 876 Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and
877 their food in a warming world. *Journal of Ornithology*, 153, 75–84.
- 878 Wiersma, P., & Piersma, T. (1994). Effects of microhabitat, flocking, climate and migratory goal on
879 energy expenditure in the annual cycle of Red knots. *Condor* 96, 257-279.
- 880 Williams, J. B., Tieleman, B. I., Visser, G. H., Ricklefs, R. E., October, N. S., Williams, J. B., &
881 Visser, G. H. (2007). Does growth rate determine the rate of metabolism in shorebird chicks
882 living in the Arctic? *Physiological and Biochemical Zoology*., 80, 500–513.
- 883 Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., Mcnamara, J. M., Levey, D. J., Partecke, J.,
884 Fudickar, A., Kacelnik, A., Roshier, D., & Piersma, T. (2014). Cues , strategies , and outcomes:

885 how migrating vertebrates track environmental change. *Movement Ecology*, 2, 10.

886 Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J.,
887 Schmidt, N. M., Gilg, O., & Roslin, T. (2015). Exposing the structure of an Arctic food web.
888 *Ecology and Evolution*, 5, 3842–3856.

889 Zhemchuzhnikov, M.K., Versluijs, T.S.L., Lameris, T.K., Reneerkens, J., Both, C. & van Gils, J.A.
890 (2021). Exploring the drivers of variation in trophic mismatches: a systematic review of long-
891 term avian studies. *Ecology & Evolution*, 11, 3710-372.

892 Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common
893 statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

894 **Tables**

895 **Table 1:** Study populations, their respective study locations and study years (with years for which
 896 arthropod data was available marked in bold), with average hatch date, arthropod peak date, relative
 897 hatch date, arthropod peak height, average arthropod abundance (arthropods per trap per day) and
 898 average temperature during chick growth. When averages are taken over multiple years, standard
 899 deviations are given.

900

Population	Location	Years	Hatch date	Arthropod peak date	Relative hatch date / rescaled	Peak height	Average abundance	Temperature during growth (°C)
Red Knot <i>C.c. islandica</i>	Princess Marie Bay, CA 79°29'N, 75°48'E	1980, 1981	7 July ± 9	14 July (1980)	-1 / 2	27.0	16.7	0.72 ± 0.06
	Alert, CA 82°30'N, 62°20'E	1992, 1993, 1994, 1999	8 July ± 8	13 July ± 10	5 ± 8 / 22 ± 8	13.2 ± 6.6	7.3 ± 3.4	1.55 ± 0.70
Red Knot <i>C.c. canutus</i>	Cape Sterlegov, RU 75°25'N, 88°59'E	1994	16 July	17 July (1994)	-1 / -10	14.4	6.1	2.28
	Knipovich Bay, RU 76°04'N, 98°32'E	1990, 1991, 2018, 2019	11 July ± 1	11 July ± 14	0 ± 16 / -6 ± 161	24.2 ± 4.5	13.6 ± 0.3	5.19 ± 1.00
Red Knot <i>C.c. rogersi</i>	Meinypilgyno, RU 62°32'N, 177°03'E	2010 - 2019	28 June ± 3	-	-	-	-	10.94 ± 0.97
Red Knot <i>C.c. roselaari</i>	Kigluaik Mountains, USA 64°50'N, 165°57'W	2010 – 2012; 2014 – 2019 (2016)	19 June ± 3	17 July (2016)	-27 / -187	12.4	6.3	10.79 ± 1.08
Great Knot <i>C. tenuirostris</i>	Upper Anadyr River, RU 64°55'N, 168°35'E	1993, 1994, 1995	29 June ± 0	21 June (1995)	8 / 23	7.2	4.4	11.82 ± 1.58
Surfbird <i>C. virgata</i>	Turquoise Lake, USA 60°48'N, 154°00'W	1997 - 1999	20 June ± 8	29 June ± 5	-9 ± 8 / -43 ± 71	13.4 ± 6.7	7.7 ± 2.6	11.73 ± 1.18

901

902 **Table 2:** (I) Parameter values for population-specific *von Bertalanffy* growth models on body mass.
903 The upper asymptote A is fixed to mean adult body mass per population, other parameter values
904 (growth rate parameter k and inflexion point T) are estimated by the model. Relative growth rate k is
905 converted to the maximum absolute growth rate K (g per day) as $K = (4 * k / 9) * A$ (Tjørve & Tjørve,
906 2017). (II) Estimated model parameter values for one overall *von Bertalanffy* growth model, using set
907 upper asymptote values as in (I), with one overall estimated parameter T ($= 6.97$) and population-
908 specific estimated parameters k .

Population	(I) Population-specific von Bertalanffy models				(II) Overall model	
	A	T	k	K	k	K
<i>C.c. islandica</i>	130	6.97	0.092	5.30	0.086	4.97
<i>C.c. canutus</i>	127	5.14	0.121	6.82	0.125	7.03
<i>C.c. rogersi</i>	122	6.24	0.113	6.12	0.110	5.93
<i>C.c. roselaari</i>	122	7.34	0.076	4.14	0.069	3.72
<i>C. tenuirostris</i>	139	7.01	0.087	5.34	0.082	5.08
<i>C. virgata</i>	154	6.45	0.094	6.41	0.092	6.29

909

910

911 **Table 3:** Generalized linear mixed models ($\Delta AIC > 10$) of the chick condition index (CC) explained
912 by relative hatch date (RHD), relative hatch date squared (RHD²), temperature during the period of
913 growth (TG), arthropod peak height (APH), average arthropod abundance (APA) and population (P),
914 including interactions (e.g. RHDxP) as fixed effects and year (Y) as a random effect. Models are
915 ordered from smallest to highest $\Delta AICc$. The best performing model is marked in **bold**, models within
916 2 $\Delta AICc$ are marked in *italics*. Models with a $\Delta AIC > 4$ can be found in Table S9, model coefficients
917 of the best performing model can be found in Table 4.

Model	degrees of freedom	Log-likelihood	AICc	$\Delta AICc$	Model weight
CC ~ P + RHD + RHD2 + TG + APA + RHDxP + RHD2xP + TGxP + APAxP + (Y) + (CI)	26	533.15	-1012.08	0.00	0.45
<i>CC ~ P + RHD + RHD2 + TG + APA + RHDxP + RHD2xP + APAxP + (Y) + (CI)</i>	22	528.14	-1010.69	1.39	0.23
<i>CC ~ P + RHD + RHD2 + TG + APH + RHDxP + RHD2xP + APHxP + (Y) + (CI)</i>	22	527.84	-1010.10	1.98	0.17
CC ~ P + RHD + RHD2 + APA + RHDxP + RHD2xP + APAxP + (Y) + (CI)	21	525.74	-1008.04	4.04	0.06
CC ~ P + RHD + RHD2 + TG + APH + RHDxP + RHD2xP + TGxP + APHxP + (Y) + (CI)	26	530.99	-1007.77	4.31	0.05
CC ~ P + RHD + RHD2 + APH + RHDxP + RHD2xP + APHxP + (Y) + (CI)	21	525.37	-1007.30	4.78	0.04

918

919

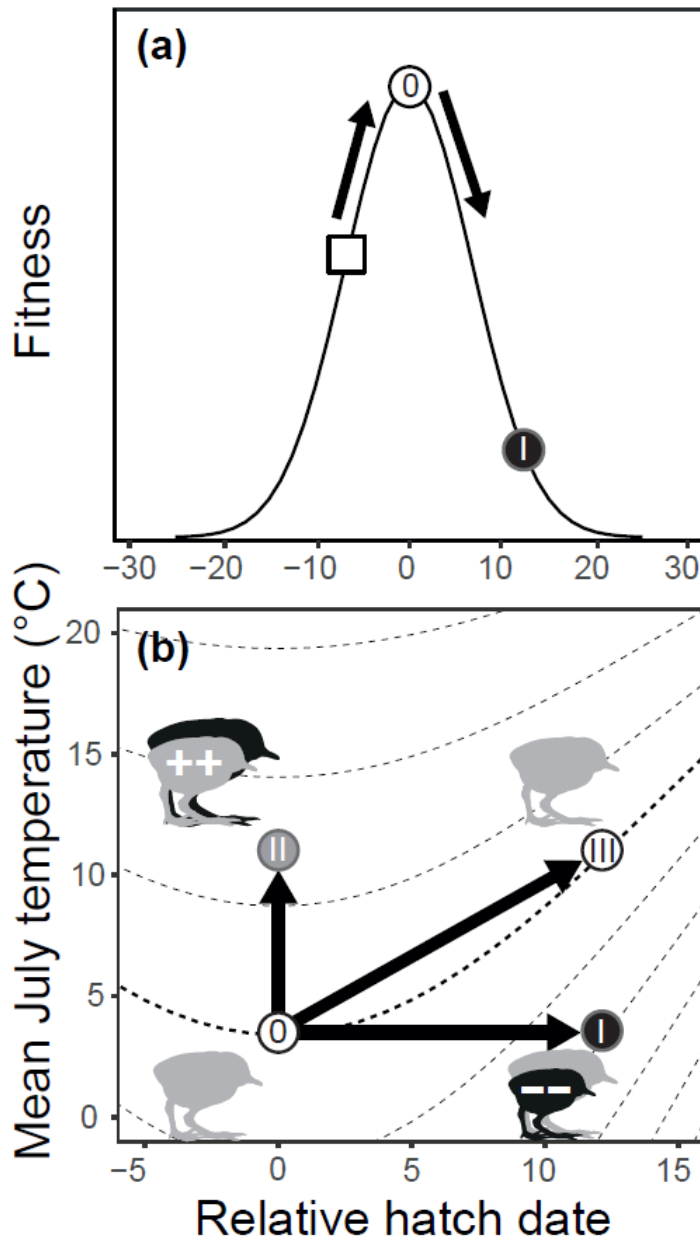
920 **Table 4:** β coefficients and 95% confidence intervals from the top model explaining chick condition
 921 with rescaled relative hatch date (RHD), rescaled relative hatch date squared, temperature during chick
 922 growth (TG) and average arthropod abundance (APA) and interactions with population. Cohen's D
 923 effect sizes are given for a simpler model, including only RHD, TG and interactions with population.

Population	β and 95% confidence intervals				Cohen's D	
	<i>RHD</i>	<i>RHD squared</i>	<i>TG</i>	<i>APA</i>	<i>RHD</i>	<i>TG</i>
<i>C.c. islandica</i>	0.73 ± 0.23 [0.27;1.18]	-24.88 ± 6.77 [-38.21;-11.56]	0.37 ± 0.15 [0.07;0.67]	0.18 ± 0.03 [0.11;0.26]	-0.34	0.83
<i>C.c. canutus</i>	-0.07 ± 0.05 [-31.01;30.87]	0.21 ± 0.28 [-0.36;0.78]	0.04 ± 0.02 [0.01;0.07]	-0.11 ± 0.04 [-740.92;740.7]	-0.31	0.21
<i>C.c. roselaari</i>	0.21 ± 0.21 [-0.21;0.63]	1.36 ± 1.09 [-0.78;3.5]	-0.05 ± 0.05 [-0.16;0.06]	-	-0.28	0.06
<i>C. tenuirostris</i>	1.25 ± 0.61 [0.04;2.46]	-57.07 ± 18.64 [-93.75;-20.4]	0.02 ± 0.03 [-0.04;0.07]	-	-0.76	0.16
<i>C. virgata</i>	-0.58 ± 0.24 [-1.07;-0.09]	-4.35 ± 1.91 [-8.12;-0.57]	0.00 ± 0.03 [-0.05;0.05]	-0.2 ± 0.1 [-0.49;0.08]	-0.23	0.09

924

925

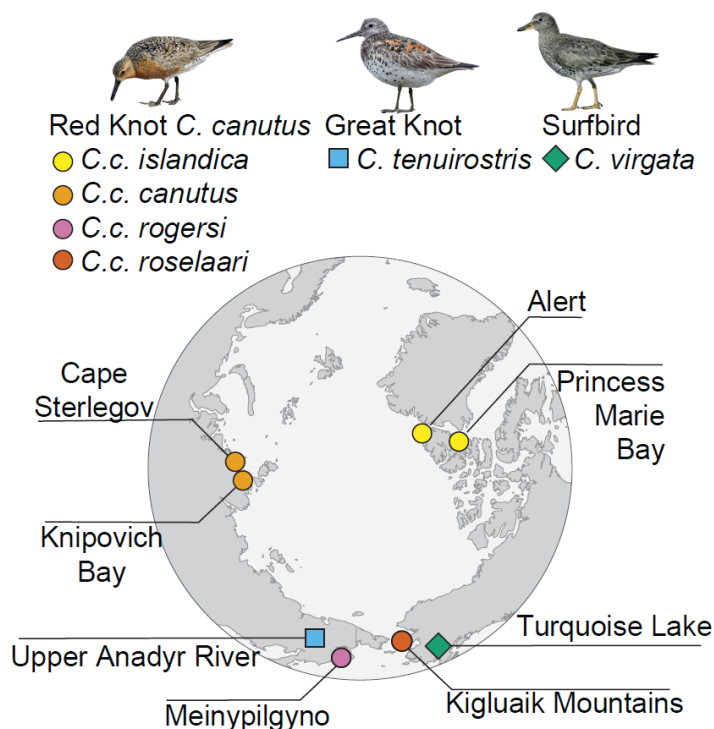
926



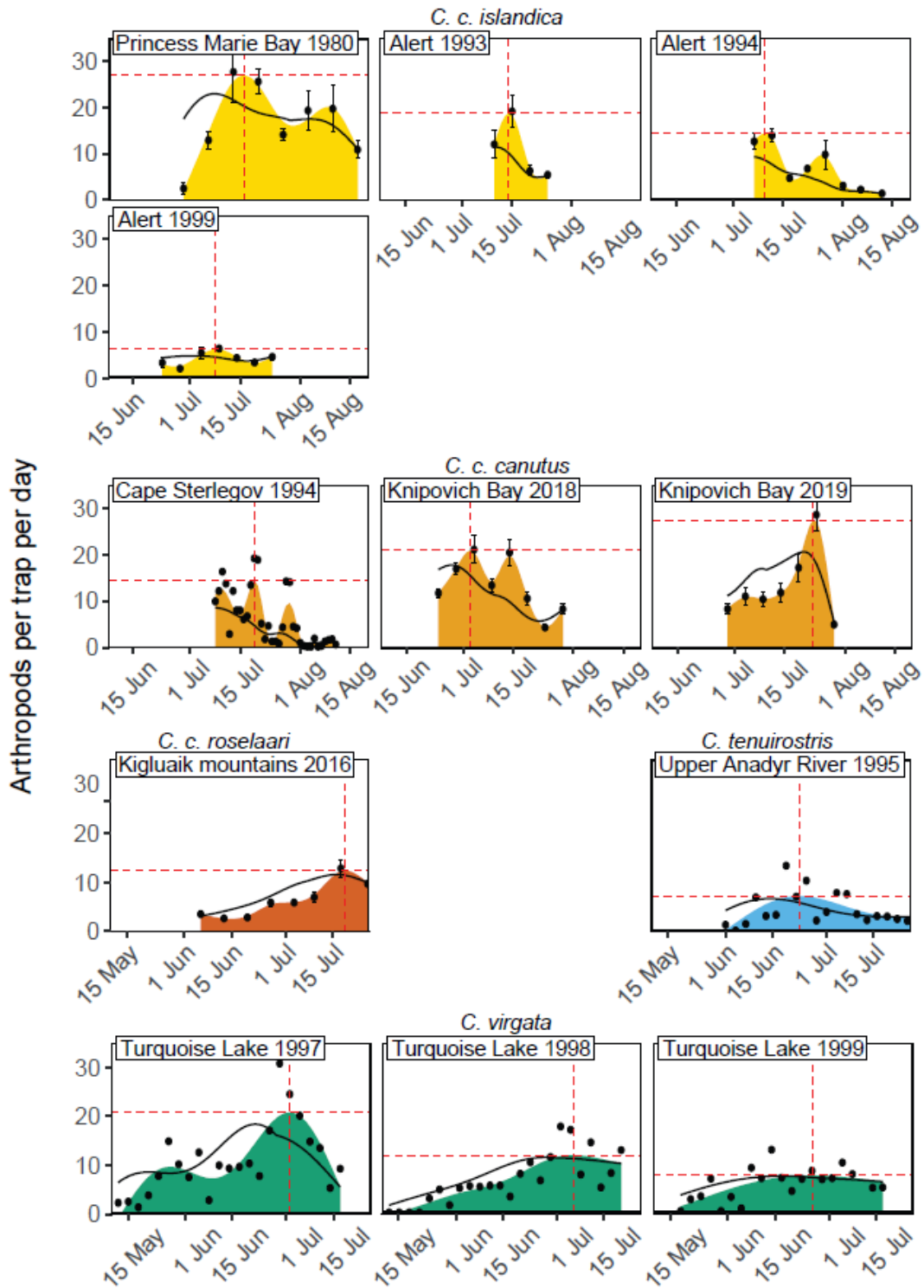
928

929 **Figure 1:** (A) We expect a unimodal relationship between relative hatch date (relative to peak food
 930 availability) and fitness (black line), with lower fitness rewards at relative hatch dates before and after
 931 an optimal match between hatch date and peak food availability (at a relative hatch date of 0). The
 932 unimodal relationship may explain differences between populations in sensitivity to trophic
 933 mismatches; populations normally hatching before the peak in food availability (white rectangle) will
 934 initially gain fitness with later hatch dates, while populations hatching currently at the peak in food
 935 availability (white dot, 0) will lose fitness with later hatch dates (black dot, I). (B) At the same time,

936 increases in temperature may ameliorate some fitness aspects such as chick growth, potentially
 937 mitigating negative effects of a later hatch dates. Iso-lines show the conceptual combined effect of
 938 relative hatch date and July temperature on chick growth, with faster growth towards the top-left (with
 939 higher temperatures and at a relative hatch date of 0), and slower growth towards the bottom-right
 940 (later relative hatch dates, lower temperatures). Under climate warming, trophic mismatches (relative
 941 hatch dates > 0) as well as temperatures are predicted to increase. If growth variation is driven only by
 942 relative hatch dates as in Fig. 1a, the growth rate of a chick currently hatching at the food peak (white
 943 dot, 0) is expected to decrease (black dot I, smaller black chick). However, if growth variation is only
 944 driven by temperatures, growth rate would increase in a warming climate (grey dot II, larger black
 945 chick). If growth rate is driven by both factors, growth rates could remain constant under climate
 946 warming, where higher temperatures mitigate the effect of later relative hatch dates (white dot III, grey
 947 chick equal in size).



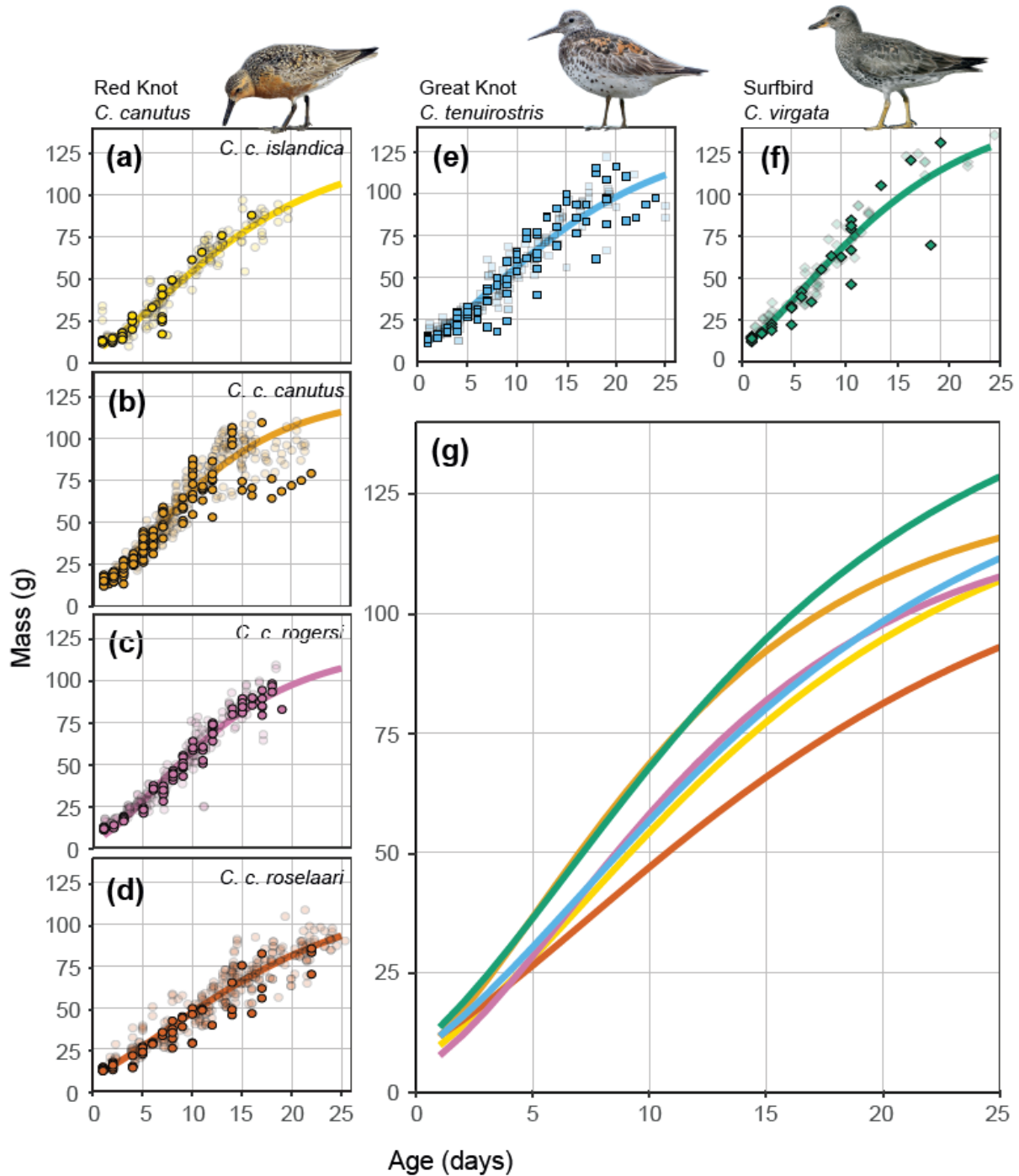
948
 949 **Figure 2:** Study locations for Red Knot ssp. *islandica* (yellow dots), *canutus* (orange dots), *rogersi*
 950 (purple dot) and *roselaari* (red dot), Great Knot (blue square) and Surfbird (green diamond).



951

952 **Figure 3:** Observed number of arthropods per trap per day (black dots with error bars showing
 953 standard errors) and predicted number of arthropods from general additive models (coloured surface),
 954 shown per year and study site for Red Knots ssp. *islandica* (yellow), *canutus* (orange) and *roselaari*
 955 (red), Great Knots (blue) and Surfbird (green). Average abundance over a 20-day chick growth period,
 956 which is used to calculate a rescaling factor, is shown by the black lines. Arthropod peak dates (date of

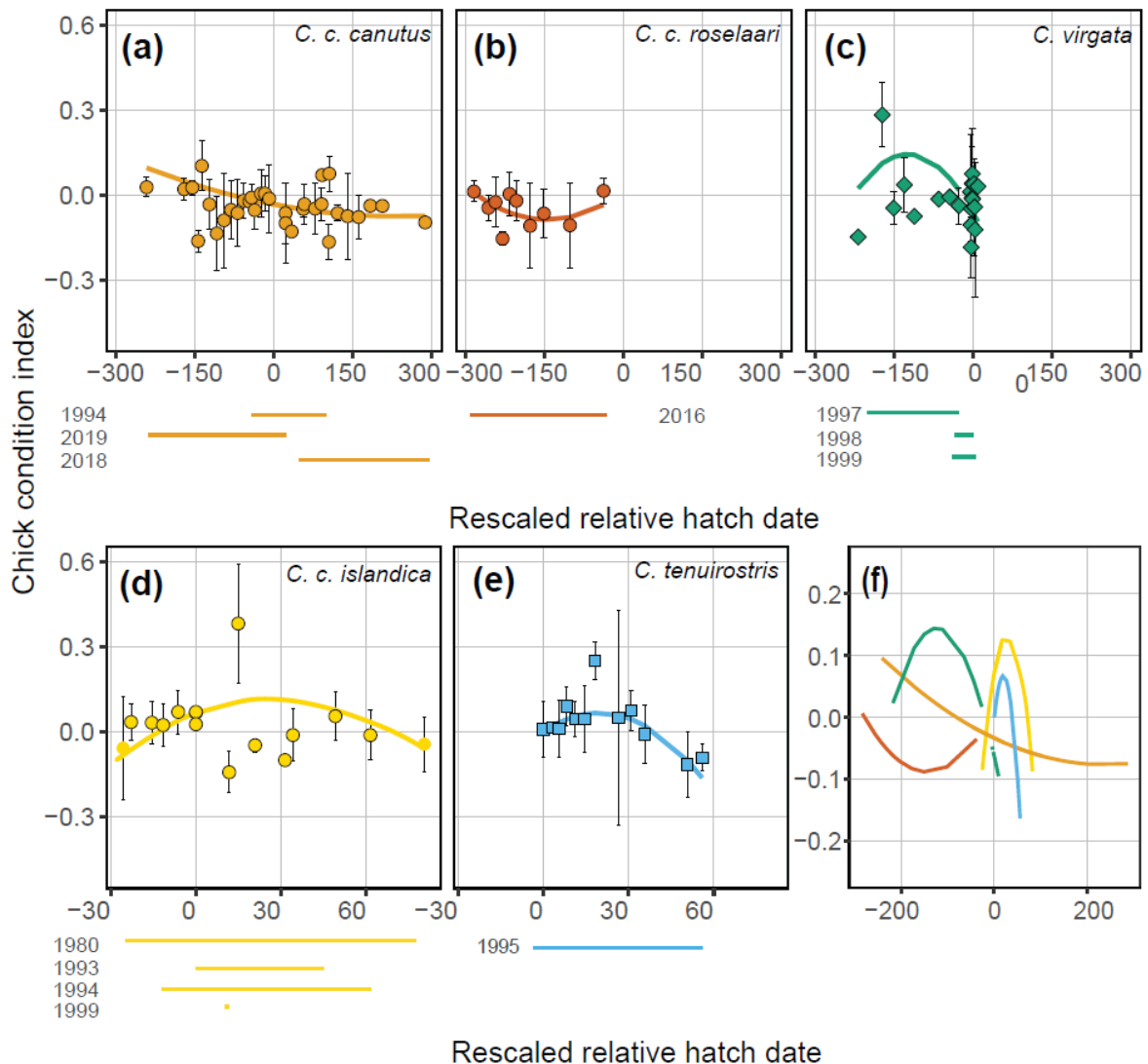
957 maximum predicted abundance) are depicted by vertical red lines, and arthropod peak height
958 (maximum abundance) is depicted by horizontal red lines.



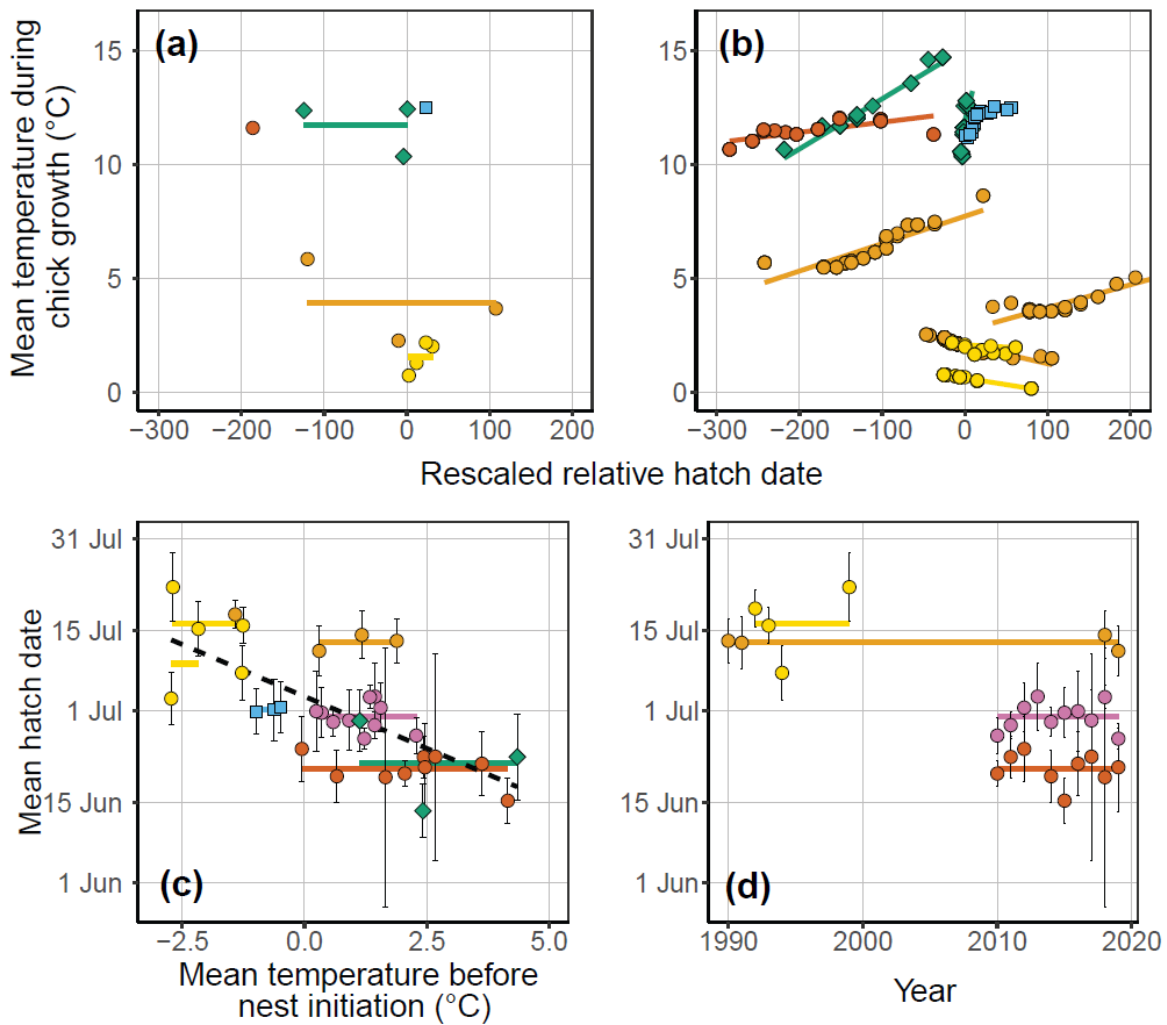
959

960 **Figure 4:** Coloured lines show body mass growth of chicks described by population-specific *von*
961 *Bertalanffy* growth models, for Red Knots ssp. *islandica* (A), *canutus* (B), *rogersi* (C), *roselaari* (D),
962 Great Knots (E), Surfbirds (F), and population-specific models of all populations plotted together (G).
963 Solid points show measurements of chicks with known age, shaded dots show measurements of chicks

964 with predicted age. Population-specific colouring and symbols are similar to Fig. 2.

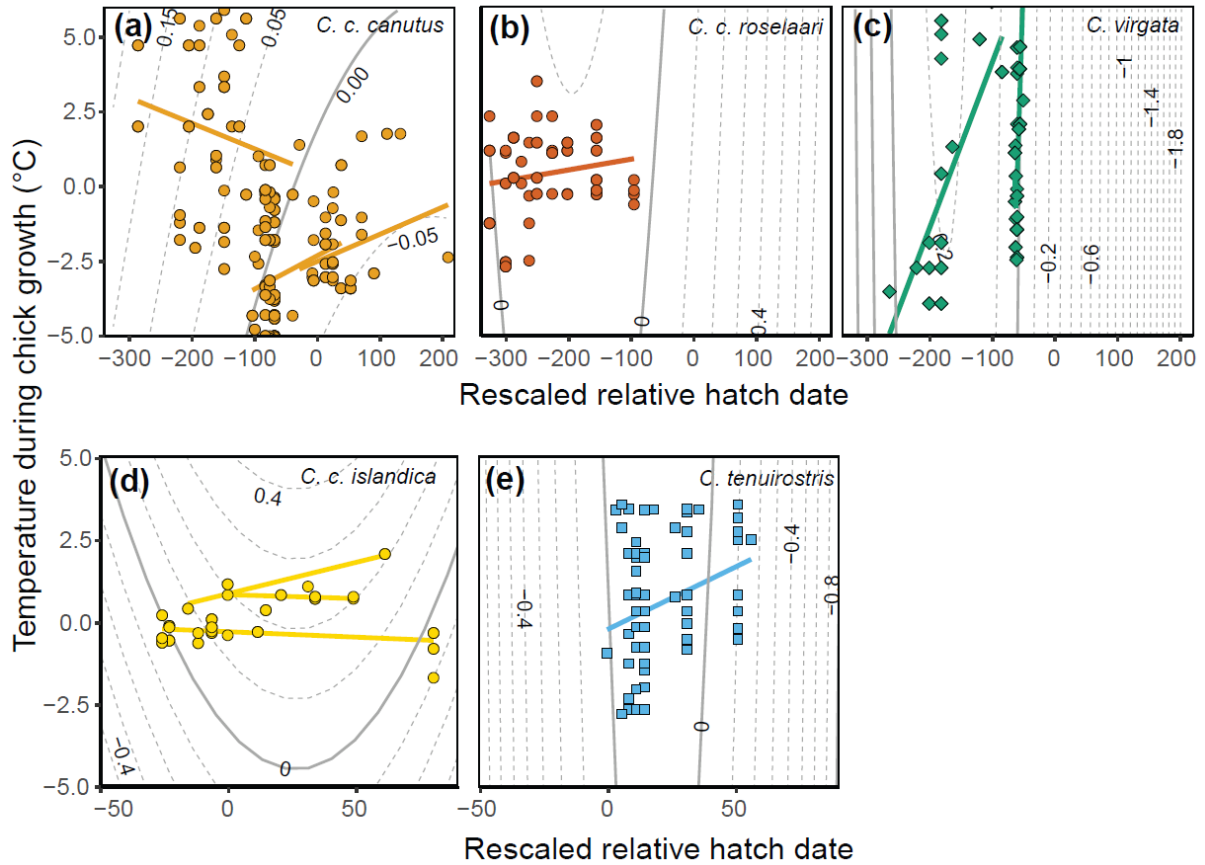


965
 966 **Figure 5:** Chick condition index plotted against the rescaled relative hatch date (plots for non-rescaled
 967 relative hatch date in Fig. S4), for Red Knots ssp. *canutus* (A), *roselaari* (B), and Surfbird (C) above,
 968 and Red Knots ssp. *islandica* (D) and Great Knots (E) below. Points show average values per day of
 969 relative hatch date, error bars show standard errors. Lines show year-specific linear regressions from
 970 model output. The distribution of rescaled relative hatch dates in different years is shown below each
 971 graph. (F) shows year-specific linear regressions for all populations for comparison. Note the different
 972 scaling in A-C, D-E and F.



973

974 **Figure 6:** (A) Rescaled relative hatch date averaged per year and population plotted against the annual
 975 mean temperature during chick growth, with coloured lines showing the population average
 976 temperature. (B) Rescaled relative hatch date and temperature during chick growth (20-day period) per
 977 individual, with coloured lines showing correlations, plotted per year. (C) Annual average hatch date
 978 per population and year with error bars showing standard deviations, plotted in relation to average
 979 temperature during the period of chick growth, with coloured lines showing population-specific
 980 averages and the black line showing across-population linear regression. (D) Annual average hatch
 981 dates for Red Knots ssp. *islandica*, *canutus*, *rogersi* and *roselaari*, plotted over years, with colours
 982 lines showing population-specific averages. Population-specific colouring and symbols in all plots are
 983 similar to Fig. 2.



984

985 **Figure 7:** (A-E) Population-specific predictions of chick condition (grey lines dotted lines, with solid
 986 line being a chick condition of 0) as predicted from the top model for values of rescaled relative hatch
 987 and temperature during chick growth for a 14 day old chick. Points show values of rescaled relative
 988 hatch date and temperature as measured for individual chicks, with population-specific colouring and
 989 symbols similar to Fig. 2. Lines show correlations between temperature and rescaled RHD, plotted per
 990 year.