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

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Abstract

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

KEYWORDS
arthropods, Great Knot, Red Knot, shorebirds, Surfbird, trophic mismatch

1 | INTRODUCTION

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

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

In theory, assuming that food is a limiting fitness outside peaks in resource availability, reductions in fitness can be expected when the consumer's demands are highest either after or before these peaks (Drent, 2006; Kharouba & Wolkovich, 2020; Perrins, 1970). Many studies on trophic mismatch focus on the timing of reproduction, where the mismatch is expressed as the difference between the seasonal time of birth or hatch and the time of a single peak in resource availability (this is the 'relative hatch/birth date'). Single resource peaks are probably rather rare, with multiple peaks throughout a season being much more common (e.g. Tulp & Schekkerman, 2008). Still, the timing of hatch relative to a peak or period of high resource abundance (including multiple peaks) appears to be an important determinant of fitness (e.g. Reed et al., 2013; Samplonius et al., 2016). In general, the highest fitness is reached at hatch dates falling

shortly before or coinciding with the peak in resource availability (Figure 1a), although multiple peaks during the season can drive more complicated patterns in fitness rewards (Machín et al., 2018). Variation in relative hatch date can explain variation in fitness within a population, as well as between populations (Figure 1a). Assuming the advancement of food peaks in a warming climate, populations with current hatch/birth dates after the food peak will face greater fitness reductions, whilst populations with current hatch/birth dates before the peak will have some leeway before fitness is reduced (and may even initially benefit from a later relative hatch date).

However, food availability is often not the only factor affecting fitness (Visser & Gienapp, 2019). For example, it has been suggested that in cold Arctic and alpine environments, growth reductions due to trophic mismatches can be mitigated by positive direct effects of increasing temperature (McKinnon et al., 2013). Below certain threshold levels (Kersten & Piersma, 1987), higher temperatures will reduce the cost of thermoregulation for endotherms such as birds. Especially for precocial chicks that forage independently immediately after hatching, the cost of thermoregulation can be considerable (Bakken et al., 2002; Schekkerman & Visser, 2001). By brooding their offspring, birds can reduce the chicks' costs of thermoregulation (Klaassen et al., 1989) and mitigate the effects of low temperature in the first week(s) after hatching (Schekkerman et al., 2003). An increase in temperature will not only reduce thermoregulatory costs, but also brooding time, allowing precocial chicks and their parents more time to forage. Furthermore, higher temperatures may also increase the activity, availability and detectability of arthropod prey (Schekkerman et al., 2003; Tulp & Schekkerman, 2008), potentially negating the short-term impact of a trophic mismatch. Such mechanisms increase the potential for growth and may (partially) compensate for the impacts of trophic mismatch in a warming climate (Figure 1b, McKinnon et al., 2013). However, as thermoregulatory costs are only one component of the energy budgets of chicks (Schekkerman & Visser, 2001), the variation therein is probably smaller than the variation in energy intake, which fully depends on prey availability that can vary by more than an order of magnitude on a short timescale (hours to days). A reduction in thermoregulation costs due to higher temperatures may, therefore, be unlikely to fully compensate for the negative effects of trophic mismatch.

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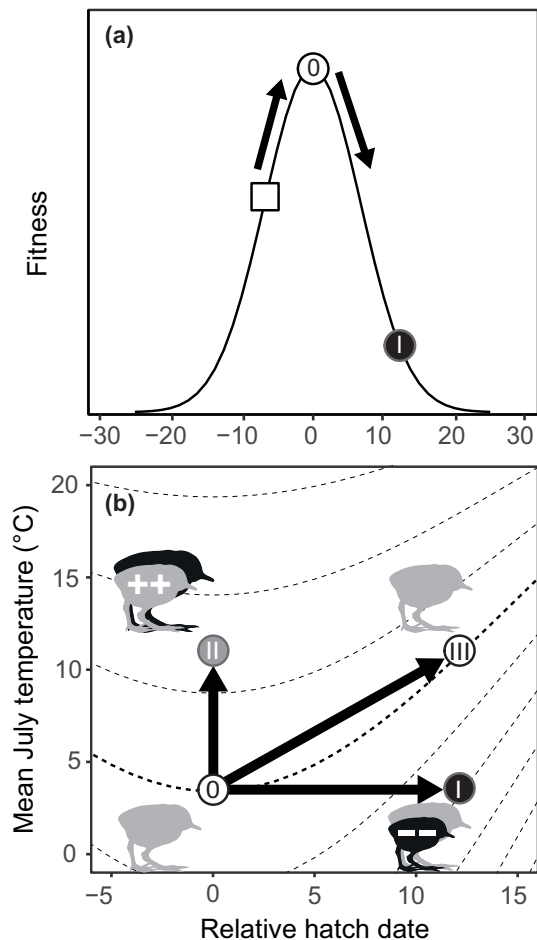
et al., 2021, but see Rakhimberdiev et al., 2018), which can result in a trophic mismatch (Kwon et al., 2019; Zhemchuzhnikov et al., 2021).

In this paper, we aim to quantify the response of chick growth to trophic mismatch and temperature in a clade of Arctic and sub-Arctic nesting Calidrine shorebirds (Gibson & Baker, 2012; Thomas et al., 2004) (Figure 2): Red Knots (*Calidris canutus*), Great Knots (*C. tenuirostris*) and Surfbirds (*C. virgata*). Together, these species have an almost circumpolar distribution, yet breed at different latitudes and elevations, thereby experiencing varying rates of climate change with potentially different impacts on chick growth. Using comparisons between and within populations, we study: (1) How populations vary in the response of chick growth to potential trophic mismatch, and (2) whether effects of mismatch can be mitigated by temperature increases. Given that Arctic-nesting shorebirds live in an environment where food is limiting outside a narrow peak of abundance (Reneerkens et al., 2016; Saalfeld et al., 2019), we expect a positive effect of later hatch dates on chick growth for populations hatching before this food peak, but negative effects for populations hatching after the food peak. We expect that temperature increases may partially mitigate such effects, especially for populations breeding in the coldest conditions. Finally, we explore (3) the potential vulnerability of populations to climate warming, by analysing trends in temperature and the trophic mismatch over time.

2 | METHODS

2.1 | Study populations and sites

We used data on hatch dates and chick growth from six breeding populations of Red Knots, Great Knots and Surfbirds. Great Knots and Surfbirds are monotypic, whilst Red Knots encompass six subspecies (reviewed

FIGURE 1 (a) We expect a unimodal relationship between relative hatch date (relative to peak food availability) and fitness (black line), with lower fitness rewards at relative hatch dates before and after an optimal match between hatch date and peak food availability (at a relative hatch date of 0). The unimodal relationship may explain differences between populations in sensitivity to trophic mismatches; populations normally hatching before the peak in food availability (white rectangle) will initially gain fitness with later hatch dates, while populations hatching currently at the peak in food availability (white dot, 0) will lose fitness with later hatch dates (black dot, I). (b) At the same time, increases in temperature may ameliorate some fitness aspects such as chick growth, potentially mitigating negative effects of later hatch dates. Iso-lines show the conceptually combined effect of relative hatch date and July temperature on chick growth, with faster growth towards the top-left (with higher temperatures and at a relative hatch date of 0), and slower growth towards the bottom-right (later relative hatch dates, lower temperatures). Under climate warming, trophic mismatches (relative hatch dates >0), as well as temperatures, are predicted to increase. If growth variation is driven only by relative hatch dates as in (a), the growth rate of a chick currently hatching at the food peak (white dot, 0) is expected to decrease (black dot I, smaller black chick). However, if growth variation is only driven by temperatures, the growth rate would increase in a warming climate (grey dot II, larger black chick). If the growth rate is driven by both factors, growth rates could remain constant under climate warming, where higher temperatures mitigate the effect of later relative hatch dates (white dot III, grey chick equal in size)
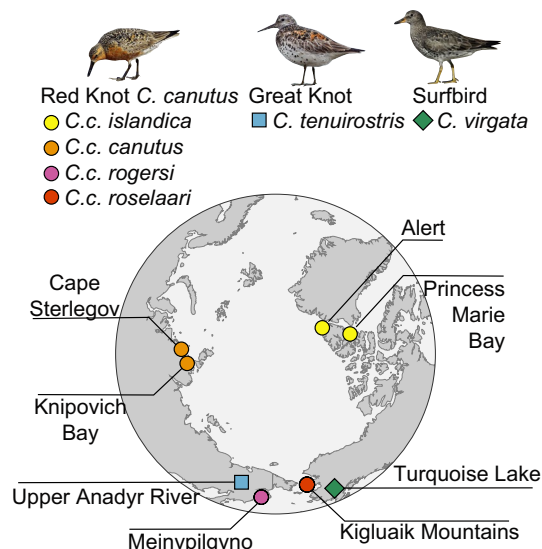

FIGURE 2 Study locations for Red Knot ssp. *islandica* (yellow dots), *canutus* (orange dots), *rogersi* (purple dot) and *roselaari* (red dot), Great Knot (blue square) and Surfbird (green diamond) [Colour figure can be viewed at wileyonlinelibrary.com]

in Piersma, 2007), of which four subspecies are included in our study, *C.c. islandica*, *C.c. canutus*, *C.c. rogersi* and *C.c. roselaari*. In our analyses, we made comparisons between and within subspecies (for Red Knots) and species (for Great Knots and Surfbirds), totalling six populations. Red Knots, Great Knots and Surfbirds are all medium-sized shorebirds, with adult body masses ranging between 122 and 154 g. Females lay a four-egg clutch, which is incubated by both parents, after which chick care is provided by the male (Red Knot and Great Knot) or by both parents (Surfbird) (Loktionov et al., 2015; Tomkovich, 1995; Tomkovich et al., 1998). Renesting attempts are rare but may occur after nest failure early in the season (Tomkovich, 1991, P. Tomkovich, J. Johnson, pers. comm.). During 21 summer seasons (ranging 3–10 per population, summing up to a total of 36 'study years', Table 1) between 1980 and 2019, these populations were studied at eight study sites with an almost circumpolar distribution (Figure 2), including sub-Arctic, low-Arctic and high-Arctic sites (Meltofte, 2013). Breeding habitats are characterized by low vegetation, classified as either montane dwarf shrub tundra (Turquoise Lake, Kigluaik Mountains and Upper Anadyr River), coastal plain with dry dwarf shrub and lichen tundra (Meinypilgyno) and Arctic tundra (Knipovich Bay, Cape Sterlegov, Alert, Princess Marie Bay).

2.2 | Data collection

2.2.1 | Hatch dates and biometric data of chicks

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

2.2.2 | Arthropod abundance data

Arthropods are the main prey of shorebirds and their chicks on their breeding grounds (Holmes & Pitelka, 1968). We used the abundance of surface-active arthropods as a measure of prey availability for shorebird chicks, which was measured for five of our study populations. Sampling methods differed between sites, but generally comprised a series of pitfall traps placed in the habitat where shorebirds foraged, which were emptied on a regular basis (daily to weekly, see Table S1 for details on methods). Trapped arthropods were counted and identified in the lab at the family level, except at Upper Anadyr River and Turquoise Lake, where the total number of trapped arthropods was counted in the field. At all sites, larval stages, Lepidoptera and bumblebees (Apidae) were excluded from the arthropod data as these are not available as prey for chicks (the former dwell underground and the latter two are too

large). Collembola were also excluded, as these were not registered at all study sites and are difficult to quantify accurately with the trapping methods used. In addition, the energetic profitability of collembola is low and preliminary data show that they hardly occur in the diet of Red Knot ssp. *canutus* chicks (M. K. Zhemchuzhnikov, pers. comm.). Abundance values were corrected for the number and diameter of pitfall traps, as well as the interval in days between measurements (Table S1). When the interval between trapping dates was more than one day, we corrected the trapping date as the median date of the trapping period. Arthropod abundance was measured at seven of the eight study sites (with the exception of Meinypilgyno), and not in all years. For our analysis on chick growth in relation to prey availability and relative hatch date, this meant that the data were available from 5 populations and 13 study years (Table 1). For all other analyses, we used all available data for all 6 populations and 36 study years (Table 1).

2.2.3 | Temperature data

Modelled air temperature at 2 m above the surface for all study locations between 1980 and 2019 was downloaded at a 6-hour resolution, for the period between 1 April and 30 September from the NCEP reanalysis numerical weather model (spatial resolution $1.875° \times 1.875°$ gaussian grid, (Kalnay et al., 1996), using the R package 'RNCEP' (Kemp et al., 2012)). The modelled temperature data were evaluated against daily average temperature records collected from a weather station (Vantage Pro2, Davis Instruments) at Knipovich Bay in 2018 and 2019, which resulted in a 0.85 Pearson correlation coefficient (Figure S1).

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

2.3 | Data preparation

2.3.1 | Estimating age of chicks with unknown hatch date

Nests of our study species are relatively difficult to find (Tomkovich & Loktionov, 2020) and many chicks were first encountered when they had already left the nest. To estimate the age of such chicks with unknown hatch dates, relationships between age and biometrics for chicks with known age were used (see Table S2 for sample sizes). As a proxy of age, we used either the 10th primary length or wing length (for Red Knot ssp. *islandica* and Red Knot ssp. *canutus* at Cape Sterlegov). We fitted logistic growth models predicting 10th primary or wing length from age separately for every population, across different years (Figure S2, Table S3) and used these to predict the age and hatch date of chicks with unknown hatch dates. Complete methods are described in the Supporting information.

TABLE 1 Study populations, their respective study locations and study years (with years for which arthropod data was available marked in bold), with average hatch date, arthropod peak date, relative hatch date, arthropod peak height, average arthropod abundance (arthropods per trap per day) and average temperature during chick growth

Population	Location	Years	Hatch date	Arthropod peak date	Relative hatch date / rescaled	Peak height	Average abundance	Temperature during growth (°C)
Red Knot C.c. islandica	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 C.c. canutus	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 C.c. rogersi	Meinypilgyno, RU 62°32'N, 177°03'E	2010 – 2019	28 June ±3	–	–	–	–	10.94 ± 0.97
Red Knot C.c. roselaari	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 C. tenuirostris	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 C. virgata	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

Note: When averages are taken over multiple years, standard deviations are given.

2.3.2 | Modelling chick growth

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

2.3.3 | Calculating prey availability and relative hatch date

As we were interested in the effect of a trophic mismatch on chick growth, we calculated (1) a direct measure of prey availability for individual chicks, as well as (2) the relative hatch date (relative to the peak in arthropod abundance) for further analyses. To this end, we first modelled the dynamics of arthropod abundance over the season using general additive models for every study site and year. We included a thin plate regression spline for the smoothing basis function with day number as a predictor variable, and with the number of knots ranging between 4 and the maximum number of observations collected throughout the season, from which the best performing model was selected. We determined the peak date in arthropod abundance (per site and year) as the date at which maximum arthropod abundance was found in the general additive models (Figure 3). We further used the predictions of arthropod abundance from the general additive models as values for daily arthropod abundance, which we log-transformed for further analyses (Schekkerman et al., 2003).

1) To calculate prey availability for individual chick observations, we first determined the period of average arthropod abundance which most impacted chick condition, by determining the best-performing sliding window using the R package 'climwin' (Bailey & van de Pol, 2016). Using a dataset of selected observations of chicks which were at least 15 days old, and a potential window size of 15 days before the day of capture, we found an optimal sliding window of average arthropod abundance between the day of capture and 3 days before (see Supporting information for details on the

analysis). We used this time window to calculate the average arthropod abundance for individual chick observations.

2) We calculated the relative hatch date for individual chicks as the difference (in days) between the hatch date and arthropod peak date for that site and year. However, the shape and steepness of arthropod peaks, as well as their height varied strongly between sites and years (Figure 3), and in order to conduct a meaningful analysis across sites and years, we needed to correct for this. To this end, the relative hatch date was multiplied with a rescaling factor that represents the same loss of arthropod availability compared to the availability at the peak date in all sites and years. We calculated this rescaling factor per individual hatch date, as the difference between the maximum arthropod abundance within the season (as predicted from general additive models) and the mean arthropod abundance during the 20-day period of growth, starting at the individual chick's hatch date (black line in Figure 3). This 20-day period was chosen as chicks become volant and independent at about 20 days (Schekkerman et al., 2003). When arthropod abundance data were not available for the entire 20-day period, the average was calculated up to the last date of available arthropod abundance data. We chose this rescaling factor based on the assumptions that I) hatch date relative to the food peak can be a reliable proxy for chick food availability (Ramakers et al., 2019), yet II) when chicks grow up under roughly the same food conditions as around the peak, they will not differ in condition from chicks hatching around the peak. For clarity, we illustrate the rescaled relative hatch dates in an example. Red Knot ssp. *islandica* chicks in Alert experience strong variability in prey dynamics around the peak arthropod date. For example, chicks hatching 5 days after the arthropod peak in 1993 face a much steeper decrease in available prey (relative to the peak) compared to chicks hatching 5 days after the peak in 1999 (Figure 3). The rescaling factors for these hatch dates and years are 13.6 in 1993 (mean abundance of 5.4 compared to peak abundance of 19.0) and 2.4 in 1999 (3.6 compared to 6.0), resulting in a rescaled relative hatch date of 68 (5 * 13.6) and 12 (5 * 2.4), respectively.

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

2.3.4 | Determining time windows for temperature dependencies

We used modelled temperature data as a predictor variable in analyses on chick condition, as well as to analyse temperature dependencies of hatch dates and arthropod peak dates. As we aimed to compare the impacts of prey availability and temperature on growth,

FIGURE 3 Observed number of arthropods per trap per day (black dots with error bars showing standard errors) and predicted number of arthropods from general additive models (coloured surface), shown per year and study site for Red Knots ssp. *islandica* (yellow), *canutus* (orange) and *roselaari* (red), Great Knots (blue) and Surfbird (green). Average abundance over a 20-day chick growth period, which is used to calculate a rescaling factor, is shown by the black lines. Arthropod peak dates (date of maximum predicted abundance) are depicted by vertical red lines, and arthropod peak heights (maximum abundance) are depicted by horizontal red lines [Colour figure can be viewed at wileyonlinelibrary.com]
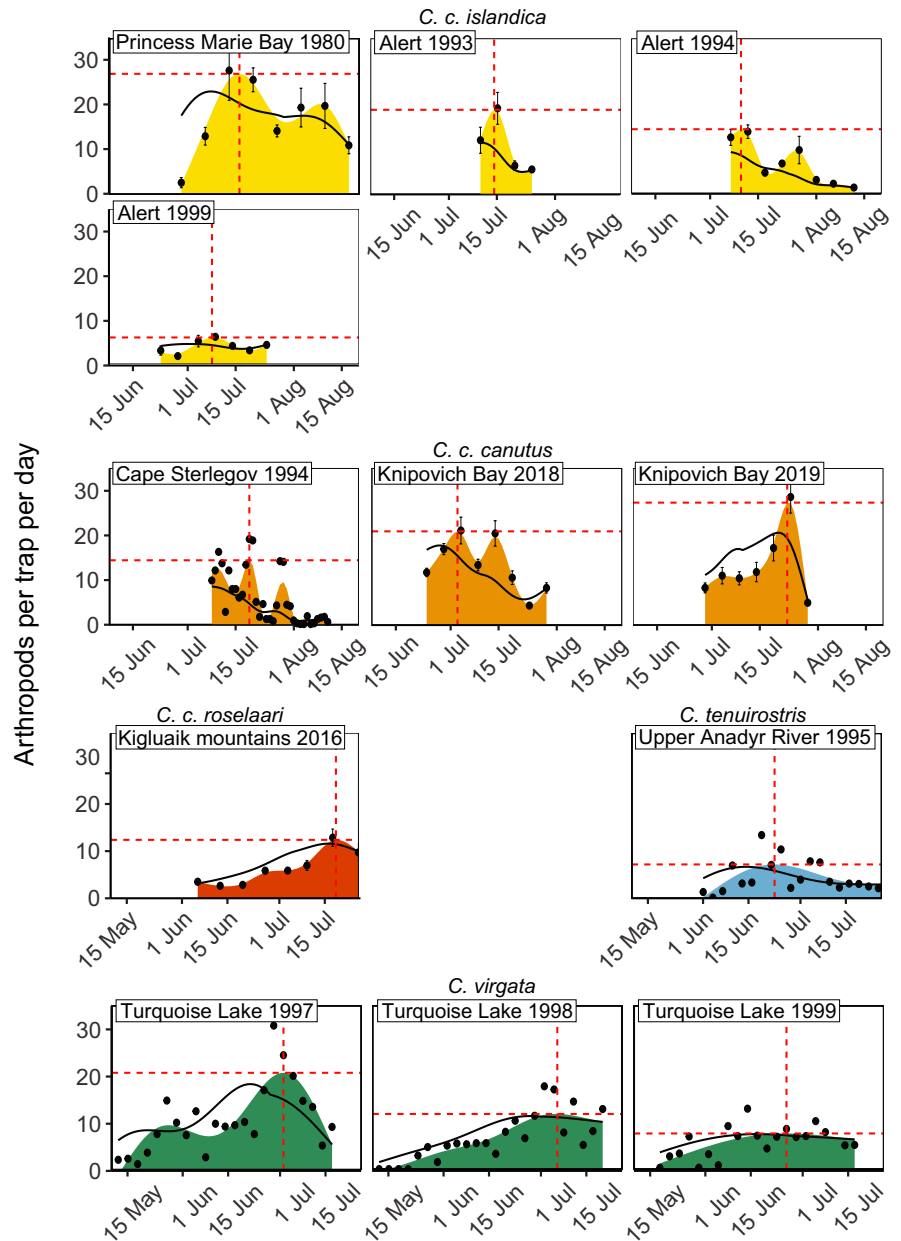
we calculated the average temperature for analyses on chick condition using the same sliding window as found for average arthropod abundance (a 3-day period before the day of capture). As we expected an effect of temperature on condition mostly within populations (with higher condition for chicks growing up under higher temperatures) rather than between populations (where faster growth is associated with lower temperatures, Tjørve et al., 2009), we standardized temperature during growth by subtracting the population-average temperature from the individual values.

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

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

To analyse the trends in temperature during chick growth, we also calculated average temperature for individual chicks during the chick growth period (20 days starting on individual chick hatch date),

as well as annual average temperature during the chick growth period (20 days starting on the annual average hatch date at the site).

2.4 | Statistical analyses

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

2.4.1 | Variation in growth rate between populations

To analyse how growth rate between populations was impacted by prey availability and temperature, we first modelled population-specific growth rate parameters k in a single *von Bertalanffy* growth model, including data of all populations, with a common parameter value for T but population-specific parameters for k (predicted by including a random effect of population on parameter k). Furthermore, a population-specific parameter A was included as well as chick identity as a random effect on k, nested within population. The performance of this model was compared to a second model that did not include population as a random effect on k. We used linear regression models to analyse how population-specific k-parameters were affected by either population-average temperature during the chick growth period, rescaled relative hatch date, average arthropod abundance or arthropod peak height, which were included as predictor variables in separate models.

2.4.2 | Variation in growth rate within populations

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

Thereafter, we used generalized linear mixed effect models to test whether chick condition was affected by the predictor variables' population, rescaled relative hatch date, rescaled relative hatch date squared (given our prediction of a unimodal response in fitness, Figure 1a), temperature during the chick growth period and arthropod peak height or annual average arthropod abundance (as these variables were strongly correlated, Pearson's correlation 0.79, $t = 25.6$, $p < .01$). We standardized all predictor variables as explained above. We included interactions of all predictor variables with population and included chick identity and population-specific year as a random intercept. Model assumptions of linearity, normality, independence and equality of variance were met, based on visual assessment of residual plots, Q–Q plots and correlograms. Variance inflation factors (VIF) ranged between 1.1 and 2.7, suggesting no problematic multicollinearity (Zuur et al., 2010). We analysed whether temperature increases could mitigate effects of trophic mismatch by comparing population-specific Cohen's D effect sizes of rescaled relative hatch date and temperature, for a model including only the predictor variables rescaled relative hatch date, the temperature during chick growth, population and the interactions with population.

2.4.3 | Correlations between temperature and relative hatch dates

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

2.4.4 | Change in temperature and relative hatch dates over years

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

We then explored potential changes in relative hatch date over time, by analysing how annual variation in hatch dates were affected by temperature. For each site, linear regression models were

constructed relating hatch date with temperature before nest initiation as a predictor variable. Thereafter, we also included the study site as a predictor variable in all models, as well as interactions between study site and temperature, to assess changes within study sites. We did not test whether annual variation in arthropod peak dates was affected by temperature, as none of the temperature windows had a significant effect (see above). For Red Knot ssp. *roselaari*, *rogersi*, *islandica* at Alert and *canutus* at Knipovich Bay at least four years of data on hatch dates were available, and we tested whether hatch dates advanced over the years in linear regression models including year and study site as predictor variables.

3 | RESULTS

3.1 | Variation in growth rate between populations

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

3.2 | Variation in growth rate within populations

Chick condition increased with prey availability (average β ± standard error: 0.11 ± 0.05 [95% confidence intervals: −0.14; 0.05]; difference between model with and without prey availability 52 AICc, Tables S7, S8), with slopes differing between populations (difference between model with and without interaction prey availability and population 24 AICc, Tables S7, S8). On average, chick condition increased by 3.8% for every additional arthropod per trap per day. Chick condition showed a unimodal response with rescaled relative hatch date (average β rescaled relative hatch date: 0.32 ± 0.29 [CI: −6.39; 7.01]; average β rescaled relative hatch date squared; −16.26 ± 6.09 [CI: −28.24; −5.65]; Figure 5, Tables 3, 4), with slopes and shapes of this relationship differing between populations (Figure 5; difference between model with and without interaction effect of rescaled relative hatch date and population 21 AICc; Tables 3, 4). Red Knot ssp. *islandica*, Great Knot and Surfbird showed an initial increase in chick condition (on average 2.7% increase in condition per later day of the hatch) followed by a reduction (on average 10.7% decrease in condition per later day of the hatch squared). Red Knot ssp. *canutus* and *roselaari* showed an initial reduction in growth (on average 1.2% reduction in condition per later day of the hatch) followed by a slight increase (on average 0.3% increase in condition per later day of the squared hatch). Chick condition increased with higher temperature during the chick growth period for some populations

(average β: 0.11 ± 0.07 [CI: −0.03; 0.25], difference between model with and without temperature 3.3 AICc, Tables 3, 4), with slopes differing between populations (difference between model with and without interaction temperature and population 13.9 AICc). On average, chick condition increased by 1.4% per °C, and notably, the increase in condition with temperature was strongest for Red Knot ssp. *islandica* (6.7% increase in condition per °C; β: 0.37 ± 0.15 [CI: 0.07; 0.67], Table 4). In addition, years with higher average arthropod abundance positively affected chicks' condition in Red Knot ssp. *islandica* (1.8% increase in condition per additional arthropod per trap per day), yet negatively in Red Knot ssp. *canutus* and Surfbird (on average 1.6% reduction in condition per additional arthropod per trap per day; difference between model with and without average arthropod abundance 35.1 AICc, the difference between model with and without interaction effect of average arthropod abundance and population 32.9 AICc, Tables 3, 4).

A comparison of population-specific Cohen's D effect sizes for temperature during chick growth and rescaled relative hatch date showed that only for Red Knot ssp. *Islandica*, the effect size of temperature (0.83) was larger than the negative effect of relative hatch date (−0.34), whilst for other populations, the effect size of temperature (average 0.13) was smaller than the negative effect of relative hatch date (average −0.39).

3.3 | Correlations between temperature and relative hatch date

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

3.4 | Changes in temperature and relative hatch date over years

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

Hatch dates differed among populations, with populations characterized by earlier hatch dates experiencing higher temperatures before nest initiation (average β ± standard error: −3.62 ± 0.57 [CI: −4.78; −2.47], difference between model including temperature and model without 25.94 AICc, Figure 6c). Within study sites and between years, hatch dates were not affected by temperatures before nest initiation (model without temperature had less degrees of freedom and 1.82 lower AICc compared to a model with, Figure 6c, Table S13). Hatch dates of Red Knots (all spp.) did not change over time (difference between model with and without year was 3.32 AICc, Table S13, Figure 6d).
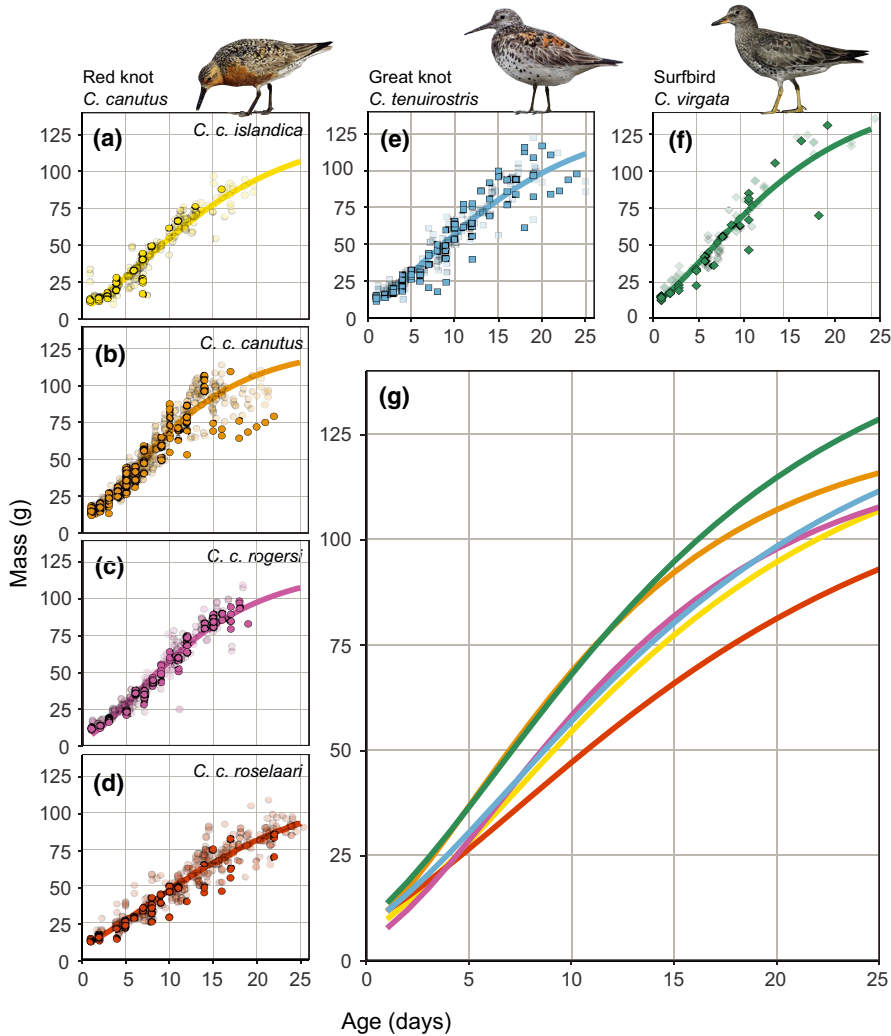
FIGURE 4 Coloured lines show body mass increase of chicks described by population-specific *von Bertalanffy* growth models, for Red Knots ssp. *islandica* (a), *canutus* (b), *rogersi* (c), *roselaari* (d), Great Knots (e), Surfbirds (f), and population-specific models of all populations plotted together (g). Solid points show measurements of chicks with known age, shaded points show measurements of chicks with predicted age. Population-specific colouring and symbols are similar to Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 (I) Parameter values for population-specific *von Bertalanffy* growth models of body mass increase, and (II) parameter values for one overall *von Bertalanffy* growth model

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

Note: In (I) the upper asymptote *A* is fixed to mean adult body mass per population, other parameter values (growth rate parameter *k* and inflexion point *T*) are estimated by the model. Relative growth rate *k* is converted to the maximum absolute growth rate *K* (g per day) as $K = (4*k/9)*A$ (Tjørve & Tjørve, 2017). In (II), the upper asymptote was set using values as in (I), with one overall estimated parameter *T* (=6.97) and population-specific estimated parameters *k*.

4 | DISCUSSION

Using comparisons between and within populations, we found that chick condition was importantly impacted by prey availability, and was highest for chicks hatching early in the season or close to the seasonal food peak. A reduction in chick condition with hatch dates falling later than the food peak signals vulnerability to trophic mismatch in almost all populations. While chick condition

FIGURE 5 Chick condition index plotted against the rescaled relative hatch date (plots for non-rescaled relative hatch date in Figure S4), for Red Knots ssp. *canutus* (a), *roselaari* (b), and Surfbird (c) above, and Red Knots ssp. *islandica* (d) and Great Knots (e) below. Points show average values per day of relative hatch date, error bars show standard errors. Lines show year-specific linear regressions from the model output. The distribution of rescaled relative hatch dates in different years is shown below each graph. (f) shows year-specific linear regressions for all populations for comparison. Note the different scaling in a-c, d-e and f [Colour figure can be viewed at wileyonlinelibrary.com]
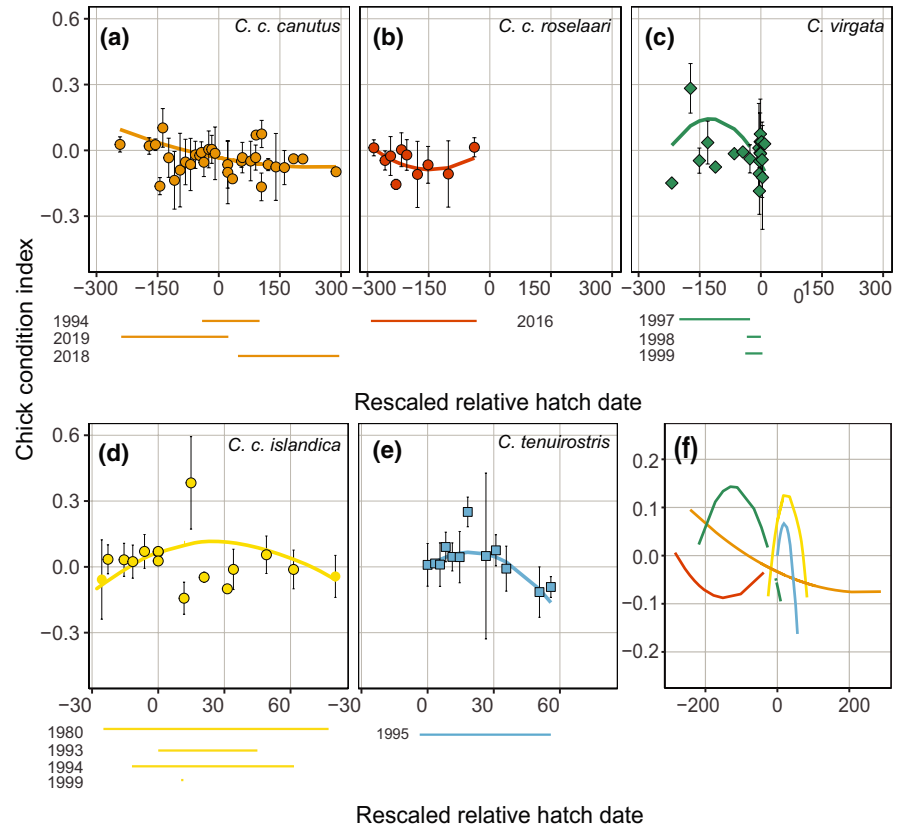

TABLE 3 Generalized linear mixed models (ΔAICc >10) of the chick condition index (CC) explained by rescaled relative hatch date (RHD), rescaled relative hatch date squared (RHD^2), the temperature during the period of growth (TG), arthropod peak height (APH), average arthropod abundance (APA) and population (P), including interactions (e.g. RHDxP) as fixed effects and year (Y) as a random effect

Model	degrees of freedom	Log-likelihood	AICc	Δ AICc	Model weight
CC ~ P + RHD + RHD2 + TG + APA + RHDxP + RHD2xP + TGxP + APAxP + (Y) + (CI)	**26**	**533.15**	**−1012.08**	**0.00**	**0.45**
CC ~ P + RHD + RHD2 + TG + APA + RHDxP + RHD2xP + APAxP + (Y) + (CI)	22	528.14	−1010.69	1.39	0.23
CC ~ P + RHD + RHD2 + TG + APH + RHDxP + RHD2xP + APHxP + (Y) + (CI)	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

Note: Models are ordered from smallest to highest ΔAICc. The best performing model is marked in **bold**, models within 2 ΔAICc are marked in *italics*. Models with a ΔAIC >4 can be found in Table S9, model coefficients of the best performing model can be found in Table 4.

generally increased with higher temperatures, temperature increases only mitigated for the effect of later relative hatch date on condition in the population of Red Knot ssp. *islandica* (Table 4), which also experienced the lowest temperatures during chick growth (Figure 5a).

4.1 | Varying responses in chick growth to a trophic mismatch between populations

We had predicted the effect of later hatching on chick growth to vary between populations, depending on whether the average chick

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

Population	β and 95% confidence intervals				Cohen's D	
	RHD	RHD squared	TG	APA	RHD	TG
C.c. islandica	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
C.c. canutus	−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
C.c. roselaari	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
C. tenuirostris	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
C. virgata	−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

in a population hatched before or after the food peak. However, hatching before or after the peak did not sufficiently explain differences in response between populations, despite strong variation in response of chick condition to relative hatch date between populations (with unimodal relationships in three out of five populations, and other populations either experiencing a seasonal decline in chick condition or a decline followed by an increase in condition). While chicks of Red Knot ssp. *canutus*, Surfbird, and partially also Red Knot ssp. *roselaari*, were in the highest condition when hatching *before* the food peak, chicks of Red Knot ssp. *islandica* and Great Knot were in the highest condition when hatching *shortly after* the food peak.

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

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

Our study faces other limitations which may reduce the strength of the analysis. First, whilst we have assumed that chicks feed on all available arthropods, they might be more specific in their diet. If chicks are specifically selecting for certain prey, this will have an important impact on the relevant peak in prey availability, and the peak date of all arthropods may be an inappropriate yardstick (Visser & Both, 2005). Incorporating specific knowledge on shorebird diet in these analyses via, for example, DNA analyses of faeces (Wirta et al., 2015), is an important (next) step in studying trophic mismatches (Cholewa & Wesołowski, 2011; Samplonius et al., 2016,
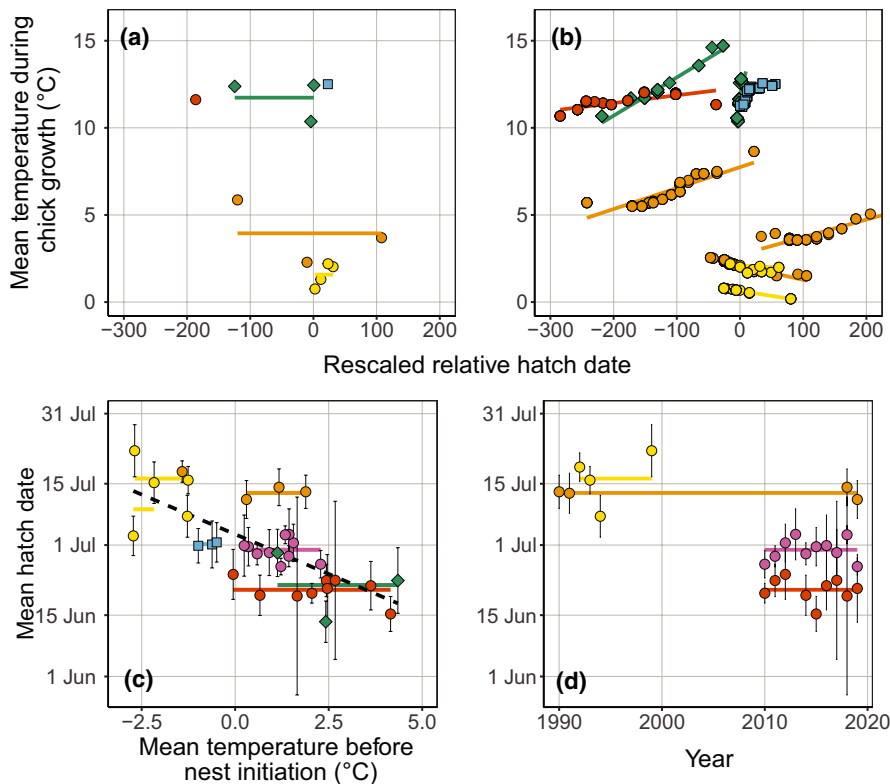
FIGURE 6 (a) Rescaled relative hatch date averaged per year and population, plotted against the annual mean temperature during chick growth, with coloured lines showing the population average temperature. (b) Rescaled relative hatch date and temperature during chick growth (20-day period) per individual, with coloured lines showing correlations, plotted per year. (c) Annual average hatch date per population and year with error bars showing standard deviations, plotted in relation to average temperature during the period of chick growth, with coloured lines showing population-specific averages and the black line showing across-population linear regression. (d) Annual average hatch dates for Red Knots ssp. *islandica, canutus, rogersi* and *roselaari*, plotted over years, with colours lines showing population-specific averages. Population-specific colouring and symbols in all plots are similar to Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

2021; Zhemchuzhnikov et al., 2021). Another limitation of our study is the use of arthropod numbers rather than biomass (as this data was not available for all populations), and the relatively low number of years with data on arthropods. These limitations may also explain the surprising result that for Surfbird and Red Knot ssp. *Canutus*, we found a negative relationship between annual average arthropod abundance and chick condition. With only 3 years of data available for these populations, this effect may well be explained by other factors varying between years. Moreover, for Red Knot ssp. *roselaari* and Great Knot, we have only one year of combined bird and arthropod data, and population and study site are confounding factors for most populations. Also, large variation exists in the years of data collection, with data from some populations only available for the 1990s, whilst data for other populations is only available from the last decade. This may limit the potential for comparative analyses. It is also noteworthy that our method of estimating age is only valid under the assumption that structural growth is unregulated by environmental conditions. Although we found strong correlations between known age and 10th primary/wing length, environmental conditions have been shown to also impact structural growth (Auer & Martin, 2017; Lloyd & Martin, 2004). However, even if chicks with

smaller structural sizes are incorrectly estimated to be of younger age, this would lead to an underestimation of the effects of temperature and relative hatch date of chick condition index due to smaller residual estimates.

4.2 | Little potential for temperature mitigating negative effects of mismatches

We found a positive effect of temperature on chick condition for some populations, with the strongest effect found for Red Knot ssp. *islandica*, yet a small effect for other populations. In general, the effects of temperature on avian growth appear to be variable (Sauve et al., 2021). When considering Arctic-nesting shorebirds, some studies have found positive effects of temperature on growth (McKinnon et al., 2013; Schekkerman et al., 1998, 2003; Tjørve et al., 2007) while other studies did not (Machín et al., 2018; Saalfeld et al., 2019) or found an effect in one year but not in the next due to annual differences in observed temperature ranges (Tulp, 2007). Physiologically, a positive effect of temperature would be expected, given that temperatures at times fall below the thermoneutral zone

(below the lower critical temperature, which is 19.9°C for adult Red Knots; Wiersma & Piersma, 1994, but probably higher for chicks; Bakken et al., 2002; Visser & Ricklefs, 1993; Visser, 1998). Chicks require more energy when facing low temperatures (Bakken et al., 2002), but may be protected from such conditions by the use of microhabitats with a protective cover (Wiersma & Piersma, 1994) or by being brooded by their parents (Krijgsveld et al., 2003; Schekkerman et al., 2003).

Chicks of Red Knot ssp. *islandica* grow up under the coldest conditions relative to other populations in this study (1.27°C compared to 10.01°C on average for all other populations). Under such conditions, low temperatures probably become a limiting factor for growth, which explains the strong positive effect of temperature on chick condition in this population. In fact, we find that for Red Knots ssp. *islandica*, the effect of temperature on chick condition is larger than that of rescaled relative hatch date, meaning that increasing temperatures may compensate for the effect of a mismatch. However, temperatures appear to be rather stable throughout the growing period of chicks, which means that there is little potential for a mitigating effect of temperatures within the season, as previously suggested (McKinnon et al., 2013). Instead, it appears that for chicks of Red Knot ssp., *islandica* mitigation can take place between years, as in years in which the trophic mismatch is larger, temperatures during growth are also higher (Figure 7, Pearson's correlation between temperature and rescaled relative hatch = 0.93, p = .07). While for most populations, food availability will be a more important determinant of energetics and growth (Schekkerman et al., 2003; Schekkerman & Visser, 2001; Senner et al., 2017) as well as survival (Saalfeld et al., 2021), temperatures appear to have an important effect on condition for chicks growing up in the coldest conditions. This means that temperatures may compensate for growth reductions induced by a trophic mismatch only under specific conditions (see also McKinnon et al., 2013), but it is unlikely that this applies as a general rule.

4.3 | Vulnerability to trophic mismatch in a warming climate

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

On the one hand, a lack of change in hatch dates over longer time periods could reflect little change in arthropod peak dates. We find that temperatures alone cannot predict arthropod peak dates, which aligns with the idea that phenology of arthropod emergence as well as activity is caused by a combination of interacting climatic variables (Koltz et al., 2018; Shaftel et al., 2021; Tulp & Schekkerman, 2008) and, therefore, is difficult to predict. Moreover, the importance of climatic variables in determining phenology may differ between invertebrate taxa (Koltz et al., 2018). Phenological advancements in arthropod emergence have nevertheless been shown in some time series (Høye et al., 2007; Rakhimberdiev et al., 2018, but see Meltofte et al., 2021) and predicted from climatic dependencies (Shaftel et al., 2021; Tulp & Schekkerman, 2008). How such advancements impact food available for shorebird chicks will
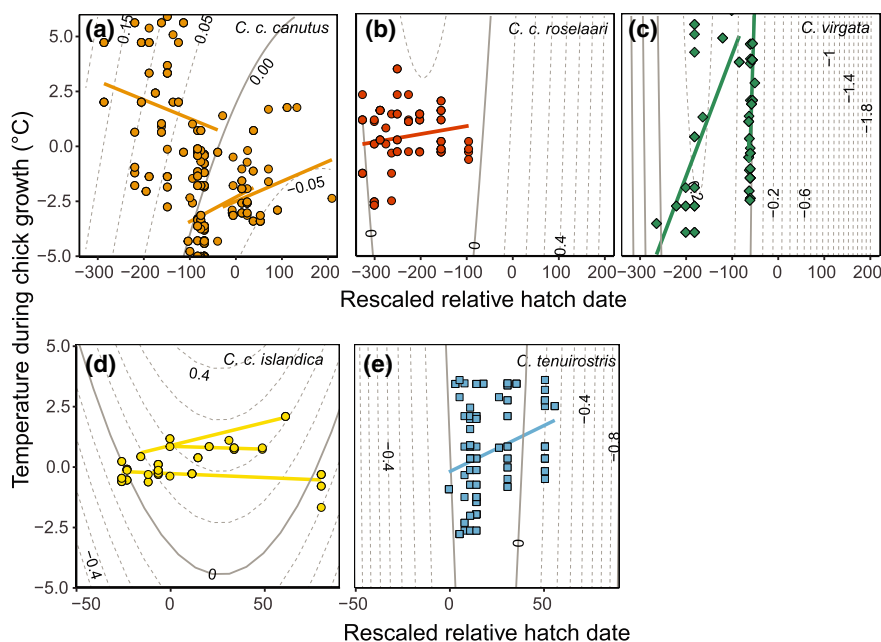

FIGURE 7 (a–e) Population-specific predictions of chick condition (grey dotted lines, with the solid line being a chick condition of 0) as predicted from the top model for values of rescaled relative hatch and temperature during chick growth for a 14-day-old chick. Points show values of rescaled relative hatch date and temperature as measured for individual chicks, with population-specific colouring and symbols similar to Figure 2. Lines show correlations between temperature and rescaled RHD, plotted per year [Colour figure can be viewed at wileyonlinelibrary.com]

also depend on climate-induced changes in arthropod community composition (Høye et al., 2021; Koltz et al., 2018), body size (Tseng et al., 2018) activity (Høye & Forchhammer, 2008), and variation in abundance outside of the peak (Machín et al., 2018; Saalfeld et al., 2019). Therefore, whether the occurrence of trophic mismatches is increasing for Arctic-nesting shorebirds is currently unclear.

On the other hand, even with advancing arthropod peaks, a lack of response in the timing of reproduction is not unexpected and is found in many migratory bird species (Knudsen et al., 2011; Samplonius et al., 2018), including many Arctic-nesting bird species (Lameris et al., 2019; Meltofte et al., 2021; Reneerkens et al., 2016; Saalfeld & Lanctot, 2017; but see Rakhimberdiev et al., 2018). This may be explained by the fact that migrants are unable to forecast changing conditions on the breeding grounds from their distant wintering grounds (Kölzsch et al., 2015; Piersma et al., 1990; Winkler et al., 2014). Also, birds may be too time-constrained to advance their timing of migration (Lameris et al., 2018, 2021b; Lindström et al., 2019; Rakhimberdiev et al., 2018), are forced to delay egg-laying in years with high snow cover (Schmidt et al., 2019) or face larger nest predation danger when initiating nests early (Borgmann et al., 2013; Byrkjedal, 1980; Meltofte et al., 2021; Reneerkens et al., 2016).

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

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

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

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REFERENCES

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Auer, S. K., & Martin, T. E. (2017). Parental care mitigates carry-over effects of poor early conditions on offspring growth. *Behavioral Ecology*, *28*, 1176–1182.

Bailey, L. D., & van de Pol, M. (2016). Climwin: An R toolbox for climate window analysis. *PLoS One*, *11*, e0167980. https://doi.org/10.1371/journal.pone.0167980

Bakken, G. S., Williams, J. B., & Ricklefs, R. E. (2002). Metabolic response to wind of downy chicks of Arctic-breeding shorebirds (Scolopacidae). *Journal of Experimental Biology*, *205*, 3435–3443. https://doi.org/10.1242/jeb.205.22.3435

Borgmann, K. L., Conway, C. J., & Morrison, M. L. (2013). Breeding phenology of birds: Mechanisms underlying seasonal declines in the risk of nest predation. *PLoS One*, *8*, e65909. https://doi.org/10.1371/journal.pone.0065909

Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, *78*, 73–83. https://doi.org/10.1111/j.1365-2656.2008.01458.x

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V., Walsh, J., Overland, J., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mard, J., Pawlak, J., & Olsen, M. S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, *14*, 045010.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*, 261–304. https://doi.org/10.1177/0049124104268644

Byrkjedal, I. (1980). Nest predation in relation to snow-cover: a possible factor influencing the start of breeding in shorebirds. *Ornis Scandinavica*, *11*, 249–252. https://doi.org/10.2307/3676131

Cholewa, M., & Wesołowski, T. (2011). Nestling food of European hole-nesting passerines: Do we know enough to test the adaptive hypotheses on breeding seasons? *Acta Ornithologica*, *46*, 105–116. https://doi.org/10.3161/000164511X625874

Corkery, C. A., Nol, E., & Mckinnon, L. (2019). No effects of asynchrony between hatching and peak food availability on chick growth in Semipalmated Plovers (*Charadrius semipalmatus*) near Churchill, Manitoba. *Polar Biology*, *42*(3), 593–601. https://doi.org/10.1007/s00300-019-02456-w

Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, *21*, 4364–4376. https://doi.org/10.1111/gcb.13057

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

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

Franks, S. E., Pearce-Higgins, J. W., Atkinson, S., Bell, J. R., Botham, M. S., Brereton, T. M., Harrington, R., & Leech, D. I. (2017). The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Global Change Biology*, *24*, 957–971. https://doi.org/10.1111/gcb.13960

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*, 2865–2873. https://doi.org/10.1002/sim.3107

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

Gill, R. E. Jr. (2022) Hatch dates and chick growth data from surfbirds (*Calidris virgata*), Turquoise Lake, Alaska, 1997-1999: U.S. Geological Survey data release. https://doi.org/10.5066/P9VDI8RZ

Holmes, R. T., & Pitelka, F. A. (1968). Food overlap among coexisting sandpipers on Northern Alaskan Tundra. *Systematic Zoology*, *17*, 305–318. https://doi.org/10.2307/2412009

Høye, T. T., & Forchhammer, M. C. (2008). The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations. *BMC Ecology*, *8*, 1–7. https://doi.org/10.1186/1472-6785-8-8

Høye, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J., & Schmidt, N. M. (2021). Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2002557117. https://doi.org/10.1073/pnas.2002557117

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid advancement of spring in the High Arctic. *Current Biology*, *17*, 449–451. https://doi.org/10.1016/j.cub.2007.04.047

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, R., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., ... Joseph, D. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, *77*, 437–471. https://doi.org/10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2

Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., & Bouten, W. (2012). RNCEP: Global weather and climate data at your fingertips. *Methods in Ecology and Evolution*, *3*, 65–70. https://doi.org/10.1111/j.2041-210X.2011.00138.x

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

Kharouba, H. M., & Wolkovich, E. M. (2020). Disconnects between ecological theory and data in phenological mismatch research. *Nature Climate Change*, *10*, 406–415. https://doi.org/10.1038/s41558-020-0752-x

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

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, *86*, 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Koltz, A. M., Schmidt, N. M., & Høye, T. T. (2018). Differential arthropod responses to warming are altering the structure of arctic communities. *Royal Society Open Science*, *5*, 171503. https://doi.org/10.1098/rsos.171503

Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K.-M., van der Jeugd, H. P., & Nolet, B. A. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *Journal of Animal Ecology*, *84*, 272–283. https://doi.org/10.1111/1365-2656.12281

Krijgsveld, K. L., Reneerkens, J. W., McNett, G. D., & Ricklefs, R. E. (2003). Time budgets and body temperatures of American golden-plover

chicks in relation to ambient temperature. *Condor*, *105*, 268–278. https://doi.org/10.1093/condor/105.2.268

Kwon, E., Weiser, E. L., Lanctot, R. B., Brown, S. C., Gates, H. R., Gilchrist, G., Kendall, S. J., Lank, D. B., Liebezeit, J. R., McKinnon, L., Nol, E., Payer, D. C., Rausch, J., Rinella, D. J., Saalfeld, S. T., Senner, N. R., Smith, P. A., Ward, D., Wisseman, R. W., & Sandercock, B. K. (2019). Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates. *Ecological Monographs*, *89*, 1–20. https://doi.org/10.1002/ecm.1383

Lameris, T. K., de Jong, M. E., Boom, M. P., van der Jeugd, H. P., Litvin, K. E., Loonen, M. J. J. E., Nolet, B. A., & Prop, J. (2019). Climate warming may affect the optimal timing of reproduction for migratory geese differently in the low and high Arctic. *Oecologia*, *191*, 1003–1014. https://doi.org/10.1007/s00442-019-04533-7

Lameris, T. K., Dokter, A. M., van der Jeugd, H. P., Bouten, W., Koster, J., Sand, S. H. H., Westerduin, C., & Nolet, B. A. (2021b). Nocturnal foraging lifts time constraints in winter for migratory geese but hardly speeds up fueling. *Behavioral Ecology*, *32*, 539–552. https://doi.org/10.1093/beheco/araa152

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

Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, *28*, 2467–2473. https://doi.org/10.1016/j.cub.2018.05.077

Liebezeit, J. R., Smith, P. A., Lanctot, R. B., Schekkerman, H., Tulp, I., Kendall, S. J., Tracy, D. M., Rodrigues, R. J., Meltofte, H., Robinson, J. A., Gratto-Trevor, C., Mccaffery, B. J., Morse, J., & Zack, S. W. (2007). Assessing the development of shorebird eggs using the flotation method: Species-specific and generalized regression models. *Condor*, *109*, 32–47. https://doi.org/10.1093/condor/109.1.32

Lindström, Å., Alerstam, T., & Hedenström, A. (2019). Faster fuelling is the key to faster migration. *Nature Climate Change*, *9*, 288–289. https://doi.org/10.1038/s41558-019-0443-7

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

Lloyd, J. D., & Martin, T. E. (2004). Nest-site preference and maternal effects on offspring growth. *Behavioral Ecology*, *15*, 816–823.

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

Machín, P., Fernández-Elipe, J., & Klaassen, R. H. G. (2018). The relative importance of food abundance and weather on the growth of a sub-arctic shorebird chick. *Behavioral Ecology and Sociobiology*, *72*. https://doi.org/10.1007/s00265-018-2457-y

Mangel, M., & Munch, S. B. (2005). A life-history perspective on short- and long-term consequences of compensatory growth. *American Naturalist*, *166*, E155–E176. https://doi.org/10.1086/444439

McKinnon, L., Nol, E., & Juillet, C. (2013). Arctic-nesting birds find physiological relief in the face of trophic constraints. *Scientific Reports*, *3*, 1–6. https://doi.org/10.1038/srep01816

Meltofte, H. (2013). What is the Arctic and who are Arctic waders? *Wader Study*, *124*, 169–171.

Meltofte, H., Hansen, J., & Rigét, F. (2021). Trends in breeding performance in wader populations at Zackenberg, high Arctic Greenland, in relation to environmental drivers 1996–2018. *Polar Biology*, *44*(10), 1939–1954. https://doi.org/10.1007/s00300-021-02922-4

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B*, *365*, 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Nettleship, D. (1974). The Breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N.W.T. *Polarforschung*, *44*, 8–26.

Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, *20*, 2221–2229. https://doi.org/10.1111/gcb.12559

Perrins, C. M. (1970). The timing of birds' breeding seasons. *Ibis*, *112*, 242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, *148*, S45–S59. https://doi.org/10.1007/s10336-007-0240-3

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

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., Ranke, J., Eispack, & R-core. (2017). Linear and nonlinear mixed effects models description. R Package, version 3, 1–336.

Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B*, *363*, 2369–2375. https://doi.org/10.1098/rstb.2007.2207

Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports*, *8*, 1–8. https://doi.org/10.1038/s41598-018-22258-0

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

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

Ramakers, J. J. C., Gienapp, P., & Visser, M. E. (2019). Comparing two measures of phenological synchrony in a predator–prey interaction: Simpler works better. *Journal of Animal Ecology*, *89*, 745–756. https://doi.org/10.1111/1365-2656.13143

Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, *82*, 131–144. https://doi.org/10.1111/j.1365-2656.2012.02020.x

Reneerkens, J., Schmidt, N. M., Gilg, O., Hansen, J., Hansen, L. H., Moreau, J., & Piersma, T. (2016). Effects of food abundance and early clutch predation on reproductive timing in a high Arctic shorebird exposed to advancements in arthropod abundance. *Ecology and Evolution*, *6*, 7375–7386. https://doi.org/10.1002/ece3.2361

Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Saalfeld, S. T., Hill, B. L., Hunter, C. M., Frost, C. J., & Lanctot, R. B. (2021). Warming Arctic summers unlikely to increase productivity of shorebirds through renesting. *Scientific Reports*, *11*, 15277. https://doi.org/10.1038/s41598-021-94788-z

Saalfeld, S. T., & Lanctot, R. B. (2017). Multispecies comparisons of adaptability to climate change: A role for life-history characteristics? *Ecology and Evolution*, 7, 10492–10502. https://doi.org/10.1002/ece3.3517

Saalfeld, S. T., Mcewen, D. C., Kesler, D. C., Butler, M. G., Cunningham, J. A., Doll, A. C., English, W. B., Gerik, D. E., Grond, K., Herzog, P., Hill, B. L., Lagassé, B. J., & Lanctot, R. B. (2019). Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecology and Evolution*, 9, 6693–6707. https://doi.org/10.1002/ece3.5248

Samplonius, J. M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S. J., Assmann, J. J., Burgess, M. D., Johansson, J., Macphie, K. H., Pearce-Higgins, J. W., Simmonds, E. G., Varpe, Ø., Weir, J. C., Childs, D. Z., Cole, E. F., Daunt, F., Hart, T., Lewis, O. T., Pettorelli, N., ... Phillimore, A. B. (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nature Ecology and Evolution*, 5, 155–164. https://doi.org/10.1038/s41559-020-01357-0

Samplonius, J. M., Bartošová, L., Burgess, M. D., Bushuev, A. V., Eeva, T., Ivankina, E. V., Kerimov, A. B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M. E., Zang, H., & Both, C. (2018). Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. *Global Change Biology*, 24, 3780–3790. https://doi.org/10.1111/gcb.14160

Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology*, 85, 1255–1264. https://doi.org/10.1111/1365-2656.12554

Sauve, D., Friesen, V. L., & Charmantier, A. (2021). The effects of weather on avian growth and implications for adaptation to climate change. *Frontiers in Ecology and Evolution*, 9, 1–20. https://doi.org/10.3389/fevo.2021.569741

Schekkerman, H., Teunissen, W., & Oosterveld, E. (2008). The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology*, 45, 1067–1075.

Schekkerman, H., Tulp, I., Piersma, T., & Visser, G. H. (2003). Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia*, 134, 332–342. https://doi.org/10.1007/s00442-002-1124-0

Schekkerman, H., van Roomen, M. W. J., & Underhill, L. G. (1998). Growth, behaviour of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. *Ardea*, 86, 153–168.

Schekkerman, H., Visser, G. H., & Blem, C. (2001). Prefledging energy requirements in shorebirds: Energetic implications of self-feeding precocial development. *The Auk*, 118, 944–957. https://doi.org/10.1093/auk/118.4.944

Schmidt, N. M., Reneerkens, J., Christensen, J. H., Olesen, M., & Roslin, T. (2019). An ecosystem-wide reproductive failure with more snow in the Arctic. *PLoS Biology*, 17, e3000392. https://doi.org/10.1371/journal.pbio.3000392

Sedinger, J. S., Flint, P. L., & Lindberg, M. S. (1995). Environmental influence on life-history traits: Growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology*, 76, 2404–2414. https://doi.org/10.2307/2265816

Senner, N. R., Stager, M., & Sandercock, B. K. (2017). Ecological mismatches are moderated by local conditions for two populations of a long- distance migratory bird. *Oikos*, 126, 61–72. https://doi.org/10.1111/oik.03325

Serreze, M. C., & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, 77, 85–96. https://doi.org/10.1016/j.gloplacha.2011.03.004

Shaftel, R., Rinella, D. J., Kwon, E., Brown, S. C., Gates, H. R., Kendall, S., Lank, D. B., Liebezeit, J. R., Payer, D. C., Rausch, J., Saalfeld, S. T., Sandercock, B. K., Smith, P. A., Ward, D. H., & Lanctot, R. B. (2021). Predictors of invertebrate biomass and rate of advancement of invertebrate phenology across eight sites in the North American Arctic. *Polar Biology*, 44, 237–257. https://doi.org/10.1007/s00300-020-02781-5

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

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241–245. https://doi.org/10.1038/nature18608

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16, 3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

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

Tjørve, K. M. C., García-Peña, G. E., & Székely, T. (2009). Chick growth rates in Charadriiformes: Comparative analyses of breeding climate, development mode and parental care. *Journal of Avian Biology*, 40, 553–558. https://doi.org/10.1111/j.1600-048X.2009.04661.x

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

Tjørve, K. M. C., & Tjørve, E. (2017). Modelling avian growth with the Unified-Richards: As exemplified by wader-chick growth. *Journal of Avian Biology*, 48, 770–784. https://doi.org/10.1111/jav.00992

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

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

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

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

Tseng, M., Kaur, K. M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., Toor, H. S., & Fograscher, K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, 87, 647–659. https://doi.org/10.1111/1365-2656.12789

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

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

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

Vatka, E., Orell, M., & Rytkönen, S. (2016). The relevance of food peak architecture in trophic interactions. *Global Change Biology*, 22, 1585–1594. https://doi.org/10.1111/gcb.13144

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

bias of traditional observational methods. *Journal of Avian Biology*, *51*, 1–12. https://doi.org/10.1111/jav.02259

Visser, G. H. (1998). Development of temperature regulation. In M. Starck, & R. Ricklefs (Eds), *Avian growth and development* (pp. 117–156). Oxford University Press.

Visser, G. H., & Ricklefs, R. E. (1993). Development of temperature regulation in shorebirds. *Physiological Zoology*, *66*, 771–792. https://doi.org/10.1086/physzool.66.5.30163823

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B*, *272*, 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research*, *35*, 89–110.

Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology and Evolution*, *12*, 879–885. https://doi.org/10.1038/s41559-019-0880-8

Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2005). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, *147*, 164–172. https://doi.org/10.1007/s00442-005-0299-6

Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, *153*, 75–84. https://doi.org/10.1007/s10336-011-0770-6

Wiersma, P., & Piersma, T. (1994). Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red knots. *Condor*, *96*, 257–279. https://doi.org/10.2307/1369313

Williams, J. B., Tieleman, B. I., Visser, G. H., Ricklefs, R. E., October, N. S., Williams, J. B., & Visser, G. H. (2007). Does growth rate determine the rate of metabolism in shorebird chicks living in the Arctic? *Physiological and Biochemical Zoology*, *80*, 500–513. https://doi.org/10.1086/520126

Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., Mcnamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D., & Piersma, T. (2014). Cues, strategies, and outcomes: How migrating

vertebrates track environmental change. *Movement Ecology*, *2*, 10. https://doi.org/10.1186/2051-3933-2-10

Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J., Schmidt, N. M., Gilg, O., & Roslin, T. (2015). Exposing the structure of an Arctic food web. *Ecology and Evolution*, *5*, 3842–3856. https://doi.org/10.1002/ece3.1647

Zhemchuzhnikov, M. K., Versluijs, T. S. L., Lameris, T. K., Reneerkens, J., Both, C., & van Gils, J. A. (2021). Exploring the drivers of variation in trophic mismatches: A systematic review of long-term avian studies. *Ecology and Evolution*, *11*, 3710–4372. https://doi.org/10.1002/ece3.7346

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

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