Trophic mismatch and its effects on the growth of young in an Arctic herbivore

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Abstract

In highly seasonal environments, timing of breeding of organisms is typically set to coincide with the period of highest resource availability. However, breeding phenology may not change at a rate sufficient to keep up with rapid changes in the environment in the wake of climate change. The lack of synchrony between the phenology of consumers and that of their resources can lead to a phenomenon called trophic mismatch, which may have important consequences on the reproductive success of herbivores. We analyzed long-term data (1991–2010) on climate, plant phenology and the reproduction of a long-distance Arctic migrant, the greater snow goose (*Chen caerulescens atlantica*), in order to examine the effects of mismatched reproduction on the growth of young. We found that geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high-quality food plants, leading to mismatches of up to 20 days between the two. The peak of nitrogen concentration in plants, an index of their nutritive quality for goslings, occurred earlier in warm springs with an early snow melt. Likewise, mismatch between hatch dates of young and date of peak nitrogen was more important in years with early snow melt. Gosling body mass and structural size at fledging was reduced when trophic mismatch was high, particularly when the difference between date of peak nitrogen concentration and hatching was >9 days. Our results support the hypothesis that trophic mismatch can negatively affect the fitness of Arctic herbivores and that this is likely to be exacerbated by rising global temperatures.

Keywords: Bylot Island, *Chen caerulescens atlantica*, climate change, nitrogen concentration, phenology, plant–herbivore interactions, snow goose, timing of breeding

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Introduction

The fast pace at which climate change is occurring (IPCC, 2013) has had measurable impacts on ecosystems and organisms by altering not only the distribution of species but also their phenology (Walther *et al.*, 2002; Root *et al.*, 2003). Indeed, phenology, defined as the timing of life history events, is probably the parameter most often affected by climate warming (Parmesan, 2006). Changes in phenology can have important consequences on trophic interactions when species at different trophic levels react to changes in their environment at different rates, a phenomenon known as trophic mismatch (Durant *et al.*, 2007). A lack of temporal synchrony between periods of high resource requirement by the consumer and periods of high food abundance can have serious population-level consequences by negatively affecting reproductive success and/or recruitment (Post & Forchhammer, 2008; Both *et al.*, 2010; Miller-Rushing *et al.*, 2010). Trophic mismatch has been

documented across multiple taxa and environments as a result of climate change, most notably in temperate passerine birds (Visser *et al.*, 1998; Both *et al.*, 2006), ungulates (Post & Forchhammer, 2008; Post *et al.*, 2008; Plard *et al.*, 2014), defoliating insects (Visser & Holleman, 2001; Schwartzberg *et al.*, 2014) and aquatic ecosystems (Edwards & Richardson, 2004; Winder & Schindler, 2004).

Polar regions are warming at a faster pace than the rest of the planet (ACIA, 2004; Barber *et al.*, 2008; Walsh *et al.*, 2011), and plant phenology in many Arctic regions is expected to change due to earlier snowmelt and/or higher temperatures during the growing season (Cleland *et al.*, 2007). Warming experiments conducted in Arctic and alpine regions have shown that plants can respond rapidly to increased temperatures by an accelerated phenology, increased growth and a greater reproductive effort (Henry & Molau, 1997; Arft *et al.*, 1999; Aerts *et al.*, 2004; Elmendorf *et al.*, 2012a; Oberbauer *et al.*, 2013), which could in turn affect herbivores that feed upon them. As summers are short in the tundra, animals have a small time window to reproduce

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and rear young, making them highly susceptible to trophic mismatch. This effect can be compounded in long-distance migrants because changes in climate occurring on the wintering grounds may occur at a different speed than those on the breeding grounds, thereby limiting their potential for adaptation to warming (Both *et al.*, 2010; Møller *et al.*, 2010).

Arctic-nesting geese are major herbivores in many tundra regions, and these long-distance migrants may be vulnerable to trophic mismatch during reproduction. Gosling growth is known to be highly sensitive to environmental conditions during the prefledging period (Gauthier *et al.*, 2006) and is directly related to the quality and availability of food plants during brood-rearing (Larsson & Forslund, 1991; Lindholm *et al.*, 1994; Lepage *et al.*, 1998). Growth of goslings is limited by protein, which is generally measured by the nitrogen concentration of plants (Sedinger & Raveling, 1986; Lepage *et al.*, 1998). Nitrogen concentration of Arctic plants typically reaches a peak shortly after the onset of plant growth followed by a constant decline throughout the summer until senescence (Chapin, 1980; Manseau & Gauthier, 1993; Piedboeuf & Gauthier, 2000). Goose reproduction is highly synchronized within the population and is timed so that hatching coincides with peak nitrogen concentration in plants (Manseau & Gauthier, 1993; Lepage *et al.*, 1998; Larter & Nagy, 2001). Should this synchrony be disrupted, growth of goslings may be negatively affected, with potentially severe consequences for population dynamics (Aubry *et al.*, 2013; Brook *et al.*, 2015). A mismatch between hatching and peak food availability has been shown to negatively affect growth in Arctic-nesting insectivorous shorebirds (McKinnon *et al.*, 2012).

We previously showed that short-term warming had a negative impact on the nutritive quality of plants for geese in the Canadian Arctic. An experimental increase of 1–2 °C caused an acceleration of the seasonal decline in plant nutritive quality and resulted in a decrease in the nitrogen concentration of plants by up to 14% during the period of gosling growth (Doiron *et al.*, 2014). Moreover, at the same study site, Dickey *et al.* (2008) have shown that gosling mass and size near fledging were reduced in years with high spring temperature. They suggested that this could result from a reduced availability of high-quality food during growth due to a lack of synchrony between hatch dates and peak nitrogen concentration in plants.

In this study, we use a 20-year dataset on climate, plant nutritive quality, goose breeding phenology, goose density and gosling growth to test the hypothesis that trophic mismatch negatively affects the reproduction of greater snow geese (*Chen caerulescens atlantica*) in the Arctic. Our aims are to determine which climatic factors affect the date of peak nitrogen in plants and the synchrony between hatching and date of peak nitrogen and to evaluate the effects of a mismatch between the two on gosling growth. We predict that (i) date of peak nitrogen will occur earlier in warm years with an early spring snow melt, (ii) the mismatch between goose breeding phenology and date of peak nitrogen concentration will increase in warm years with an early snow melt and (iii) this mismatch will negatively impact body mass and size of goslings at fledging.

Materials and methods

Study area

This study took place on the south plain of Bylot Island (73°08′N, 80°00′W), north of Baffin Island, Nunavut, Canada. This region is characterized by flat lowlands surrounded by extensive upland plateaus covered with lush tundra vegetation for its latitude. The south plain of Bylot Island is one of the most important breeding areas for the greater snow goose, a colonial nester (Reed *et al.*, 2002). It is the only goose species nesting in the area except for a few cackling geese (*Branta hutchinsii*). During nesting, geese are mainly localized in a relatively small area (ca. 50 km^2), but during brood-rearing adults with goslings disperse throughout most of the south plain (ca. 1600 km^2). The habitats used by geese can be divided into two broad categories (Gauthier *et al.*, 1996). The first habitat type consists of freshwater wetlands characterized by wet polygon fens (Tarnocai & Zoltai, 1988) dominated by grasses and sedges, such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe and, to a lesser extent, *Carex aquatilis* Wahlenb., growing through a thick carpet of brown mosses. This habitat is highly homogeneous as these three species combined make up >97% of the herbaceous plant cover (Manseau & Gauthier, 1993; Gauthier *et al.*, 1995). The second habitat type consists of upland mesic tundra, characterized by rolling hills and better drained soil where vegetation is more diversified and dominated by prostrate shrubs, graminoids and other small herbaceous species. Although comprising only about 15% of the landscape, wetland polygon fens are highly preferred by geese and are used at high density during nesting and most of the brood-rearing period (Hughes *et al.*, 1994; Mainguy *et al.*, 2006). Lemmings are the only other significant herbivores in the area as large herbivores (muskox *Ovibos moschatus* and caribou *Rangifer tarandus*) are absent. In this area, the average spring temperature has increased by 2.8 °C over a 35-year period (Gauthier *et al.*, 2011), and the annual cumulative number of thawing degree-days (i.e. sum of daily mean air temperature above zero) has increased from 381 to 521 between 1989 and 2011 (Gauthier *et al.*, 2013).

Climatic data

Since 1994, a fully automated weather station located in the Qarlikturvik Valley, a large glacial valley near the north end of the south plain, has been recording air temperature at 2 m above the ground on an hourly basis (CEN, 2013). Daily rain-

fall was collected manually with a rain gauge from 1 June to 15 August from 1995 to 2010. We also obtained temperature and rainfall data from the Environment Canada weather station located at the Pond Inlet airport on Baffin Island, approximately 80 km south-east of the Qarlikturvik Valley. Weather data from those two stations were highly correlated over the period of 1994–2004, which allowed us to estimate local temperatures and rainfall between the years 1991 and 1993 (see Dickey *et al.*, 2008), thus extending our data to cover 1991–2010. Each year, snow melt was monitored at 2-day intervals by visually estimating percent snow cover from a vantage point from 1 June until complete snow melt.

We extracted the date at which snow cover first reached 50% of the landscape as a proxy of snow-melt phenology. We defined two periods, spring (20 May to 20 June), which corresponds to the arrival, prelaying and laying period of geese, and summer (20 June to 15 August), which corresponds mostly to the incubation and brood-rearing periods. From the temperature data, we extracted the following variables: average, maximum and minimum temperature (expressed as mean of daily average, maximum and minimum values for each period), and sum of thawing degree-days. For each time period (spring and summer), we performed a principal component (PC) analysis based on the aforementioned temperature variables and extracted individual scores along the first axis as an index (PC score) of temperature. In all PC analyses, the first axis explained >71% of variation and the variables had loadings of >0.69 on this axis (see Table S1). A high PC score was associated with warm conditions and a low one with cool conditions. Total annual rainfall was also calculated for spring (1 June to 20 June, as no rain data was available for earlier dates) and summer (20 June to 15 August) for all years except 1994 (no data available for that year).

We retrieved daily Arctic Oscillation (AO) and North Atlantic Oscillation (NAO) values from the Climate Prediction Center of the National Weather Service (http://www.cpc.ncep.noaa.gov/) and calculated annual average values for spring (20 May to 20 June) and summer (20 June to 15 August). The AO is a nearly axisymmetric spatial pattern of sea-level pressure centered over the Arctic (Thompson & Wallace, 1998). NAO can be considered a regional manifestation of AO, and both have been linked to climate and biological processes at our site (Dickey *et al.*, 2008; Bêty *et al.*, 2014). NAO and AO values were strongly correlated within each time period ($r > 0.70$), and in this study, we used the AO index for all analyses. In our study area, the AO explains more than half of the increase in winter surface air temperature (Rigor *et al.*, 2000), and positive AO values are associated with low temperatures and precipitations in winter (Hurrell, 1995; JISAO, 2004). Although the AO is primarily viewed as a winter phenomenon, it shows similar patterns of change in atmospheric pressure in the summer months but with less vigorous variation (Serreze *et al.*, 1997; Aanes *et al.*, 2002).

Plant biomass and nitrogen data

Aboveground live biomass in wetlands (polygon fens) was sampled at roughly 2-week intervals in 1991, 1993–1996 and 2006–2010. Each year, 12 new goose exclosures (1 or 4 m^2 depending on year) were set up in the Qarlikturvik Valley just after snow melt in June, before any significant grazing by geese had occurred. Exclosures were made of 30-cm high chicken wire (2.5-cm mesh) and were set up over an area of ~1 km^2. Plant samples were collected inside exclosures at least 4 times per season from mid-June to mid-August. In most years, the first sampling date occurred shortly after snow melt. Each time, we removed a 20 cm × 20 cm piece of turf at random but avoided to collect samples adjacent to previously removed pieces of turf to prevent edge effect. Vascular plants were cut at the base of the white basal stem buried in the moss. Plants were sorted into four categories: grasses (mostly *D. fisheri*), cottongrass sedges (*E. scheuchzeri*), *Carex* sedges (*Carex* spp.) and dicotyledonous plants (<2%; mostly *Stellaria longipes*, *Saxifraga* sp. and *Salix* spp.). Samples were sorted out into vegetative green parts (i.e. leaves), flowers (including stems) and dead matter (which was discarded), oven-dried at 45 °C for 36 h and weighed to the nearest 0.001 g [see Gauthier *et al.* (1995) for details].

We analyzed the nutritive quality of only *Dupontia* and *Eriophorum* because these plants are by far the most abundant in wetlands of the study area and are preferred by geese due to their high nutritive quality (Manseau & Gauthier, 1993; Gauthier *et al.*, 1995). The vegetative green parts of each species were ground to a fine powder and analyzed separately for total nitrogen concentration. Between 1991 and 1996, the samples were analyzed using an automated macro-Kjeldahl analyser (Kjell-Foss, model 16210) following the AOAC (1984, p. 154) method (Gauthier *et al.*, 1995). From 2006 onwards, nitrogen concentration was determined using a QuickChem Lachat nutrient auto-analyser (QuickChem 4000 Series; Zellweger Analytics, Milwaukee, WI, USA). In some cases, it was necessary to pool samples from different exclosures (but collected at the same date) to obtain sufficient material for the nitrogen analyses. Date of peak nitrogen was extracted from the relationship between plant nitrogen concentration and date of the season [see Doiron *et al.* (2013) for details]. For each sampling date, we used the mean nitrogen concentration measured in both plant species (i.e. *Dupontia* and *Eriophorum*), giving equal weight to each species in the calculation. Nitrogen biomass was calculated as the product of green biomass by nitrogen concentration in each individual sample.

A previous study by Doiron *et al.* (2013) showed that the date at which 50% of the annual maximum Normalized Difference Vegetation Index (NDVI) is attained is a good predictor of the date of peak nitrogen concentration in graminoid plants at our study site. As nitrogen was only directly measured during 10 years (1991, 1993–1996, 2006–2010), we used the equation of Doiron *et al.* (2013) to predict peak nitrogen date for an additional 10 years, extending our time series to cover the entire time period of 1991–2010. NDVI data were obtained from the Canada Centre for Remote Sensing (Pouliot *et al.*, 2009) and were derived from the Advanced Very High Resolution Radiometer of the National Oceanic and Atmospheric Administration satellites [see Doiron *et al.* (2013) for details]. As NDVI was not an accurate predictor of actual maximum nitrogen concentration (%) or maximum nitrogen biomass

$(g\ m^{-2})$ in plants, our time series for these two variables are comprised of only 10 years.

Goose reproductive data

Goose breeding biology has been monitored in our study area since 1989. Each spring, several hundred nests (>350 in all years but one) initiated throughout the laying period are found in the colony and monitored. Nests are revisited near hatching to determine hatch date (defined as the date when ≥50% of the eggs hatched) and to mark goslings in the nest with web tags [see Lepage *et al.* (2000) for details]. Approximately 5 weeks after hatching, before fledging, goose families were captured in mass banding drives over a 7- to 10- day period. Nonbreeders and failed breeders do not stay on Bylot Island to molt and thus birds captured at banding were almost exclusively successful breeders (Reed *et al.*, 2003). The majority of captures were made in the Qarlik- turvik Valley, although in most years, some captures were also made in neighboring valleys. Captured goslings were sexed by cloacal examination and the majority of them, including all web-tagged goslings recaptured, were weighed (nearest 25 g in 1991–1994, nearest 1 g from 1995 onward) and measured with callipers (culmen, head and tarsus length to the nearest 0.1 mm). An average of 105 (ranging from 17 to 275) web-tagged goslings were recaptured and measured each year, for a total of 2096 individuals from 1115 different families. All captured adults and goslings were released together at the end of each banding drive.

In order to account for potential density-dependent effects on the growth of goslings, we computed three annual indices of goose density on the breeding ground: feces count, young to adult ratio at banding and nest density in the colony. The feces counts were obtained from 12 annual transects (1 × 10 m) located near the grazing exclosures. We removed all feces already present when exclosures were installed in mid-June and counted all feces present at 2-week intervals. We calculated an annual average value from the cumulative number of feces counted on each transect at the end of the summer. Young to adult ratio values were obtained from the average ratio of young to adult in each banding drive. Nest density was based on the annual number of nests found in a defined area (9.64 ha) located in the center of the colony and systematically searched each year.

Statistical analyses

Using simple linear regressions, we first examined the relationship between median hatch date of goslings and annual date of peak nitrogen concentration in plants. We defined the mismatch between geese and plants as the difference (in days) between hatch date of goslings and date of peak nitrogen concentration. We also determined which climatic variables best explained the annual variation in four variables related to plant nitrogen: date of peak nitrogen concentration, maximum nitrogen concentration, maximum nitrogen biomass and mismatch. All climatic variables tested (along with their Pearson's r values) are presented in Table S2. As we used annual values

and because the periods covered for each variable did not always fully overlap, sample sizes were small ($n = 9$–20), and thus, we were limited in the number of climatic variables we could simultaneously test in our linear models. To counter this, we did not include in the model more than four variables together in cases when $n = 19$–20 and three variables when $n = 9$–10, and retested them along with their interactions in several combinations of the variables.

We then examined the combined effects of plant nitrogen and climatic variables on the body mass and size of goslings. To compare the mass and size of goslings, it was necessary to correct for the age at which they were measured. Indeed, both year and age as well as their interaction explained a significant amount of variation in goslings mass and size ($P < 0.001$ in all cases). For each individual, we thus added the residuals (i.e. the difference between observed and predicted values) to the mean overall mass and body size measurements predicted by the model for each year at 35 days (average age at capture) and used these values for subsequent analysis. To determine structural size of goslings, we performed a PC analysis based on the measurements of head, culmen and tarsus length and used the individual scores as an index of size [see Lepage *et al.* (1998) for details]. The first axis explained >92% of total variation, and all variables had loadings of >0.9 on this axis (see Table S3).

We used hierarchical mixed models to determine which variables had an effect on individual measures of gosling mass and size (procedure PROC MIXED of SAS 9.3; following the method outlined in Bell *et al.*, 2013). Multilevel models were necessary because of the hierarchical nature of our data set: The dependent variables (gosling mass and size) and mismatch (number of days between hatch date and annual date of peak nitrogen) were at the individual level (level 1), whereas the other variables (nitrogen, climatic and density variables; see Table S2 for the full list) were single annual values (level 2). This approach allowed us to account for the possible dependence among individuals, as all goslings hatched each year were exposed to the same environmental conditions. Additionally, the variable *family* was included in the models as a random effect to account for the dependence (genetic and environmental) between goslings originating from the same nest. Because some of the variables were highly correlated (Table S2), we reran the same analyses multiple times using only one of the correlated variables at a time (when $r \geq 0.60$). We further tested our models for multicollinearity by calculating the variance inflation factor (VIF) of the predictors used in each model and considered that multicollinearity was not an issue because all VIF were <3 (Zuur *et al.*, 2010). As rainfall values were missing in 1994, this year was excluded from the multilevel models.

Model selection was based on the AICc statistics, starting from the most complex models and removing variables to obtain the models that best explained the variation in each dependent variable. The model with the lowest AICc value was considered the most parsimonious, and those with differences of <2 AICc units were considered well supported by the data (Burnham & Anderson, 2002). To examine the possibility that relationships between gosling mass/size and plant

phenology could depend upon a threshold, we compared models with linear, quadratic or piecewise (segmented linear) effects of mismatch and date of peak nitrogen. The break point for the piecewise models was chosen by comparing a series of models using different break points along the x-axis and selecting the model with the lowest AICc value.

As we only had 9 years of data for maximum nitrogen concentration and maximum nitrogen biomass (vs. 19 years for all other variables), we repeated the previous analysis with only 9 years of data in order to include these variables. For these years, mismatch with the date of peak nitrogen concentration was calculated solely from empirical data rather than with a mixture of empirical data and values estimated from the linear equation with NDVI (described above). Therefore, this smaller dataset also served to validate the results obtained with the 19-year data set. Conditional R^2 values were calculated following the procedure outlined by Nakagawa & Schielzeth (2013). Statistical analyses were performed with R (R Development Core Team, 2006) and SAS (SAS Institute, Cary, NC, USA).

Results

Annual variations in plant and goose phenology

Over the 20-year period, the date of peak nitrogen concentration in plants showed considerable variation. Peak nitrogen occurred over a 27-day period, ranging from 17 June to 14 July, with a mean date of 29 June [day of the year (DOY) 180 ± 6.9; Fig. 1a]. Goose breeding phenology showed much less variation, as annual median hatch date spanned a 13-day period from 3 to 16 July, with a mean median date of 9 July (DOY 190 ± 3.2 days; Fig. 1a). There was little overlap between these two variables, and in all but two years, median hatch date occurred after date of peak nitrogen in plants. There was a significant positive relationship between median hatch date and date of peak nitrogen (Fig. 1b), with a regression slope of 0.25 (95% CI: 0.06, 0.44). The annual gap between median hatch date of goslings and date of peak nitrogen (i.e. mismatch) varied from −2 to 20 days, with a mean value of 9.5 ± 5.8 days.

Maximum nitrogen concentration in plants varied from 2.7% to 3.7% (mean = 3.3 ± 0.3%) over the 10 years it was measured. Maximum nitrogen biomass varied from 0.5 to 1.1 g m^{-2} (mean = 0.8 ± 0.2 g m^{-2}) and occurred on average on 19 July ± 9 days. There was a weak negative relationship between peak nitrogen concentration and date of peak nitrogen in plants ($\beta = -0.02$; $R^2 = 0.25$; $F = 4.09$; $df = 9$; $P = 0.078$) suggesting that maximum nitrogen concentration (%) in plants tended to be higher in years when the date of the peak occurred earlier in the season. Maximum nitrogen biomass was not related to date of peak nitrogen ($P = 0.74$).
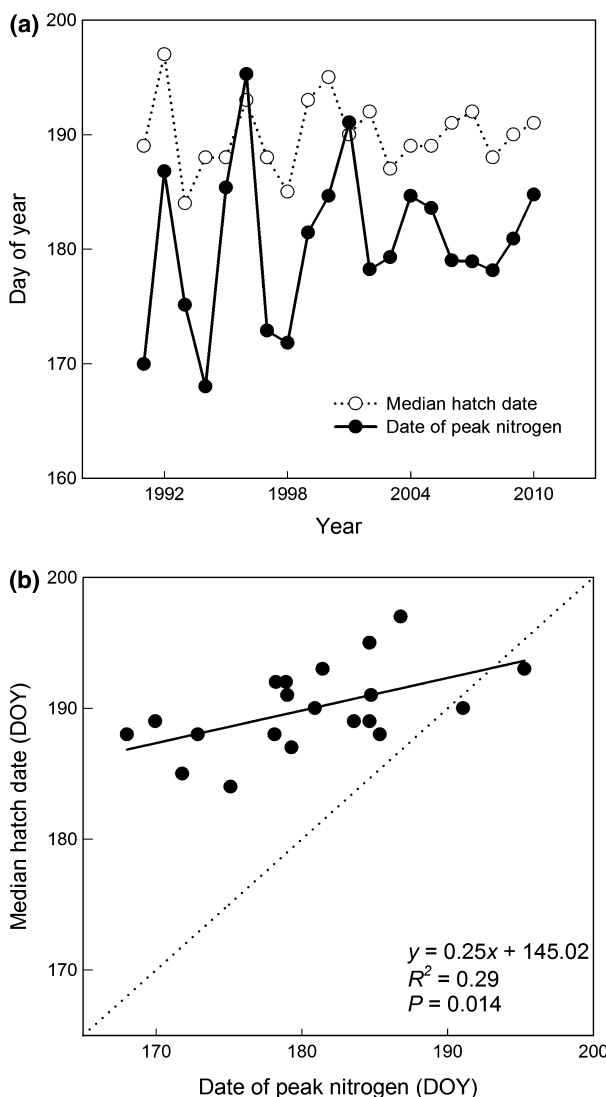

Fig. 1 (a) Annual variation in median hatching date of snow goose goslings and date of peak nitrogen concentration in their food plants on Bylot Island, NU, from 1991 to 2010. (b) Linear relationship between median hatch date and date of peak nitrogen concentration in plants. The dotted line represents a 1 : 1 line. If gosling hatch date perfectly tracked plant phenology, the data points would fall on the dotted line. Dates are in day of the year.

Effects of climate on plant nitrogen and mismatch

Only two climatic variables explained a significant proportion of variation in date of peak nitrogen concentration in plants. Date of peak nitrogen was negatively related to the spring temperature index (Fig. 2a; $\beta = -2.07$, 95% CI: −3.42, −0.70) but positively related to the date of 50% snow melt (Fig. 2b; $\beta = 0.80$, 95% CI: 0.48, 1.13). These two climatic variables were correlated ($r = -0.66$), and the model with date of 50% snow melt
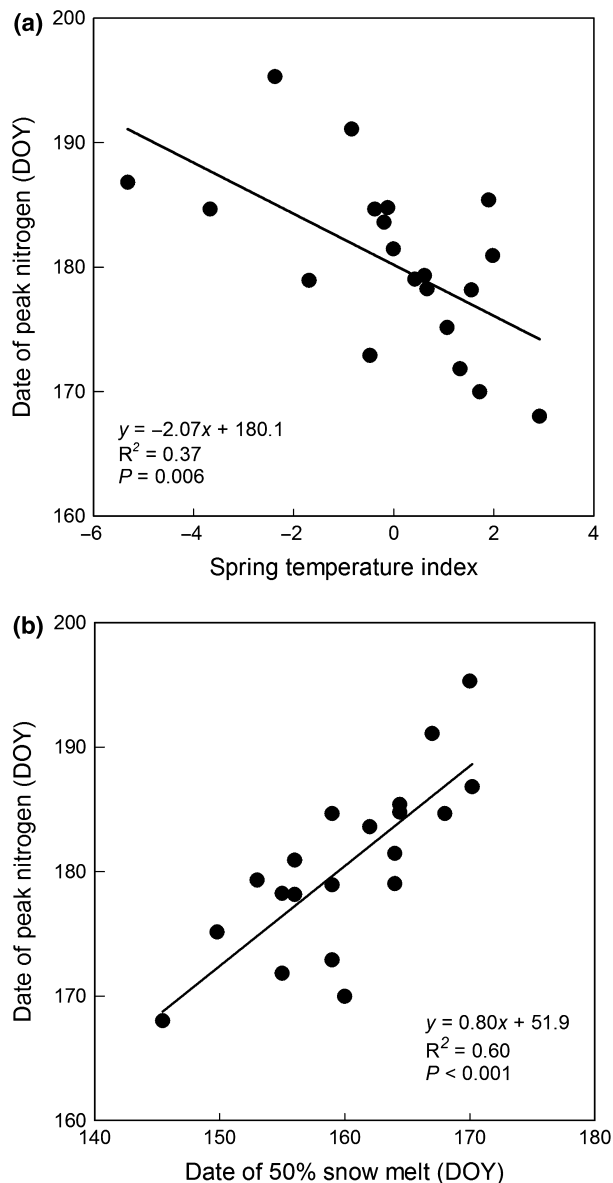
(a)

$y = -2.07x + 180.1$
$R^2 = 0.37$
$P = 0.006$

(b)

$y = 0.80x + 51.9$
$R^2 = 0.60$
$P < 0.001$

Fig. 2 Relationships between date of peak nitrogen concentration in plants and (a) spring temperature and (b) date of 50% snow melt on Bylot Island, NU, from 1991 to 2010. Spring temperature index was obtained from a principal component analysis combining temperature data (mean, maximum and minimum temperature and sum of thawing degree-days) between 20 May and 20 June. Dates are in day of the year.

$y = -0.46x + 83.6$
$R^2 = 0.28$
$P = 0.016$

- - - *Without 1994*
$y = -0.37x + 68.7$
$R^2 = 0.16$
$P = 0.088$

Fig. 3 Relationship between mismatch and date of 50% snow melt on Bylot Island, NU, from 1991 to 2010. Mismatch is defined as the difference (in days) between annual median hatch date of goslings and date of peak nitrogen concentration in plants. The relationship is presented with and without 1994 (white circle) because this year was influential on its statistical significance. Dates are in day of the year.

and $P = 0.003$) and summer AO (Fig. S1b; $y = -0.31x + 0.77$, $R^2 = 0.57$, $F = 10.47$, df $= 9$ and $P = 0.012$). Maximum nitrogen concentration was not related to any of the climatic variables.

Effect of mismatch on gosling growth

The best-supported hierarchical model explaining individual body mass of goslings included mismatch with a break point at 9 days, spring AO, summer rain and summer AO (Table 1). Individual body mass was negatively related to the mismatch, and this effect was more pronounced when this mismatch was >9 days (Fig. 4a). Body mass was also negatively related to summer rain and summer AO values but positively related to spring AO values (Table 1). There was a significant positive relationship between date of peak nitrogen and gosling body mass (Fig. 4b; β = 6.5, 95% CI: 1.2 and 11.8), but models where mismatch was replaced by date of peak nitrogen concentration performed more poorly (ΔAICc > 44.5). None of the density variables (feces count, young to adult ratio at banding, nest density in the colony) were retained in any of the preferred models (ΔAICc > 9.1). Conditional R^2 values of the top-ranked models were >0.69. When we reran the analysis with only 9 years of data (the years for which we had empirical nitrogen values), the best model included a

provided the best fit to our data (ΔAICc = 9.5 vs. spring temperature index). The annual mismatch was related to the timing of snow melt (date of 50% snow melt: $R^2 = 0.28$, $F = 6.99$, df = 19 and $P = 0.016$) with mismatch being larger in years with earlier snow melt (Fig. 3; β = −0.46, 95% CI: −0.83, −0.09). Annual maximum nitrogen biomass was significantly related to two climatic variables: summer temperature (Fig. S1a; $y = 0.10x + 0.74$, $R^2 = 0.68$, $F = 17.40$, df = 9
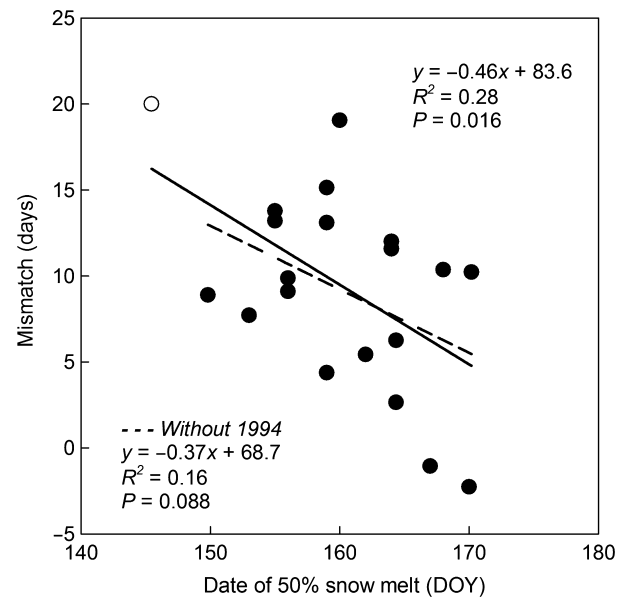
Table 1 (a) Parameters along with sign of the effect, log-likelihood value (LL), number of estimated parameters (*k*), ΔAICc values, AICc weights (ωi) and conditional R^2 values of the most parsimonious models explaining variation in gosling body mass at 35 days on Bylot Island, NU, from 1991 to 1993 and 1995 to 2010 (19 years, *n* = 2025). Goose family ID was used as a random factor in the analysis. (b) Parameter estimates of the best model and their 95% confidence interval (CI)

(a)

Model	*k*	LL	ΔAICc	ωi	R^2
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain	10	−13 162	0.00	0.41	0.68
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain +SummerTemp	11	−13 161	1.20	0.23	0.68
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain −SpringTemp	11	−13 162	1.81	0.17	0.68
−Mismatch +SpringAO −SummerAO −SummerRain	9	−13 164	2.79	0.10	0.69
−Mismatch −Mismatch² +SpringAO −SummerAO −SummerRain	10	−13 163	3.02	0.09	0.68
Null model	3	−13 336	334.70	0.00	

(b)

Parameter	Slope	95% CI
Mismatch<9	−6.5	−12.0, −1.0
Mismatch ≥9	−10.6	−14.2, −7.0
SpringAO	120.2	67.8, 172.6
SummerAO	−123.3	−209.2, −37.4
SummerRain	−1.5	−2.6, −0.4

negative linear effect of mismatch, a positive effect of summer temperature index and spring AO and a negative effect of summer rain (Table S4). A piecewise model with a break point at 8 days was a close competitor.

The best-supported hierarchical model explaining individual structural size of goslings retained the same variables as for body mass (mismatch with a break point at 9 days, summer rain and spring and summer AO, Table 2). However, in contrast to body mass, the negative effect of mismatch on body size was only significant when mismatch was >9 days (Fig. 5a). Again, none of the density variables were retained in any of the preferred models for gosling structural size (ΔAICc > 6.8). Conditional R^2 values of top-ranked models were >0.67. Models where mismatch was replaced by date of peak nitrogen concentration performed more poorly (ΔAICc > 30.2), and while the parameter estimate for this effect was positive (Fig. 5b), the confidence interval of the slope did not exclude 0 (β = 0.02, 95% CI: −0.03, 0.07). In the analysis based on only 9 years of data, the best-supported model again included a negative effect of mismatch and a negative effect of summer rain, but also a positive effect of summer temperature, whereas summer and spring AO were not retained (Table S5). As with body mass, a piecewise model with a break point at 8 days was a close competitor.

Discussion

Our results provided support for all our initial predictions: date of peak nitrogen concentration occurred earlier in warm years with early snow melt; in those years, the mismatch between goose and plant phenology increased; finally, gosling growth was negatively affected by this trophic mismatch, particularly when it reached a threshold of 9 days.

Annual variations in goose and plant phenology

The phenology of plants (date of peak nitrogen concentration) and geese (median hatch date) in our study area both showed important interannual variability. Although there was a positive relationship between the two, the slope of 0.25 shows that geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high-quality food, leading to trophic mismatches of up to 20 days in early years. This was expected as long-distance migrants are known to be relatively inflexible in their response to advances in spring phenology and are thus potentially the most susceptible to trophic mismatch among avian species (Bauer *et al.*, 2008; Both *et al.*, 2010; Clausen & Clausen, 2013). As climate change can occur at different speeds or even in opposite directions at different staging areas along the migratory route, the ability of these birds to adapt to changes in their environment may be limited.

The migration of geese is composed of several long-distance flights divided by stopover periods when they accumulate fat reserves, and environmental conditions encountered on these sites can affect the migratory decisions of individuals (Bauer *et al.*, 2008; Duriez *et al.*, 2009; van Wijk *et al.*, 2012). If they cannot acquire sufficient nutrients at stopover sites or if the weather is
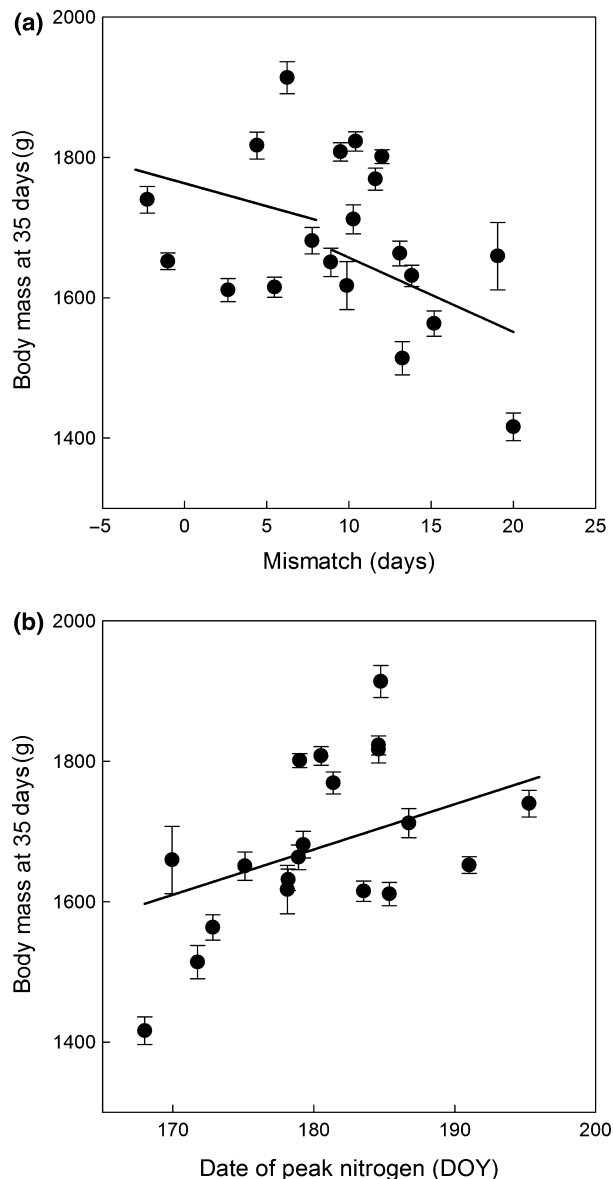
Fig. 4 Relationships between body mass of goslings adjusted at 35 days and (a) mismatch between median hatch date and date of peak nitrogen concentration in plants and (b) date of peak nitrogen concentration in plants (after controlling for climate effects) on Bylot Island, NU, from 1991 to 2010. Analyses were carried out on individual gosling measurements, but mean annual values with SE are shown to illustrate the fit of the model. Dates are in day of the year.

mismatch in thick-billed murres (*Uria lomvia*) breeding in Hudson Bay (Gaston *et al.*, 2009). In our study population, breeding females tracked by radio transmitters showed relatively high repeatability in their arrival dates on the breeding site, which implies that this trait may be characteristic of individuals in this species (Bêty *et al.*, 2004). Moreover, the time for incubating eggs is fixed (24 days in snow geese), and thus, breeding individuals are unable to advance their phenology once eggs are laid, whereas plant phenology can continue to be affected by increased temperatures during that time window (Doiron *et al.*, 2014).

The advancement in the date of peak nitrogen concentration of plants in warm years was presumably due to an early onset of plant growth, as warm temperatures and early snow melt have previously been linked to advanced phenology of Arctic plants (Wipf & Rixen, 2010; Oberbauer *et al.*, 2013; Doiron *et al.*, 2014). Warm temperatures have also been shown to accelerate plant growth: At our study site, aboveground biomass of plants was correlated to sum of thawing degree-days (Gauthier *et al.*, 2013), and warming experiments at other sites throughout the High Arctic have demonstrated that warm temperatures increase plant production (Rustad *et al.*, 2001; Elmendorf *et al.*, 2012a,b). A large mismatch typically occurred in years when the date of peak nitrogen was reached earlier than the long-term average, and mismatch was greater in years of early snow melt. Both egg laying (Dickey *et al.*, 2008) and the onset of plant growth (Wipf & Rixen, 2010) are limited by snow melt in spring. However, plants appear to track the disappearance of snow more quickly than geese as they adjust their laying date by only 0.38 days for every day of advance in snow melt (Gauthier *et al.*, 2013).

Although the date of peak nitrogen concentration was highly variable, the value of the peak itself changed very little between years, reaching 3–3.5% and declining sharply thereafter (Doiron *et al.*, 2013). Maximum nitrogen biomass (the product of nitrogen concentration and plant biomass) was lower in years with cool summer temperatures (both at the local and at the regional scales, as indexed by high AO values), probably as a result of lower vegetative growth in those years (Gauthier *et al.*, 2013). However, for growing goslings, nitrogen concentration is thought to be more important than total nitrogen biomass, which is supported by our results. Unlike most other herbivores, geese have a rapid throughput time in their gut resulting in a low digestive efficiency (i.e. they do not digest plant fiber) and have a low nitrogen retention rate (Mattocks, 1971; Sedinger, 1997). Growing goslings, which must synthesize a large amount of new tissues, depend on food with high nitrogen concentration to meet their protein

inclement, birds may be unable to arrive on the breeding sites at the optimal time for nesting and may be further delayed in laying eggs if they need to replenish energy once on the breeding site (Gauthier *et al.*, 2003). As geese are long-lived birds, the timing of egg laying may also be partly determined by learned or inherited mechanisms related to photoperiod or other invariant cues, which has been suggested as a potential cause for

Table 2 (a) Parameters along with sign of the effect, log-likelihood value (LL), number of estimated parameters (k), ΔAICc values, AICc weights (ωi) and conditional R^2 values of the most parsimonious models explaining variation in gosling body size at 35 days on Bylot Island, NU, from 1991 to 1993 and 1995 to 2010 (19 years, n = 2019). Goose family ID was used as a random factor in the analysis. (b) Parameter estimates of the best model and their 95% confidence interval (CI). Body size was obtained from the principal component score of head, culmen and tarsus length measurements

(a)

Model	k	LL	ΔAICc	ω_i	R^2
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain	10	−3325	0.00	0.41	0.66
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain −SnowMelt	11	−3324	0.37	0.34	0.65
−Mismatch(<9) −Mismatch(≥9) +SpringAO −SummerAO −SummerRain +SummerTemp	11	−3325	1.87	0.16	0.66
−Mismatch −Mismatch^2 +SpringAO −SummerAO −SummerRain	10	−3328	4.38	0.05	0.66
−Mismatch +SpringAO −SummerAO −SummerRain	9	−3329	4.55	0.04	0.67
Null model	3	−3504	343.90	0.00	

(b)

Parameter	Slope	95% CI
Mismatch<9	−0.03	−0.08, 0.01
Mismatch ≥9	−0.07	−0.1, −0.04
SpringAO	0.7	0.2, 1.1
SummerAO	−1.1	−1.9, −0.4
SummerRain	−0.01	−0.02, −0.004

requirement as they cannot compensate a reduction in nitrogen concentration by increasing food intake (Sedinger, 1997; Richman *et al.*, 2015).

Effect of mismatch and climate on growth of young

Gosling body mass and structural size near fledging were reduced when there was a mismatch between date of peak nitrogen concentration and individual hatch date. The effect of this mismatch was more pronounced when it exceeded ~9 days, probably because feeding conditions of goslings deteriorate rapidly after that. Indeed, we showed in a previous study that (i) the nitrogen concentration of graminoid plants at our study site reaches a peak in late June/early July, after which it decreases rapidly to about half its peak levels 15–20 days later, and (ii) this decline is more abrupt when the temperature is increased (Doiron *et al.*, 2014). Thus, goslings hatched late in the season have access to food of much lower quality (i.e. lower nitrogen concentration, more fiber content). The effect of a mismatch on the mass and size of gosling near fledging can have major fitness consequences, as smaller goslings have lower chances of surviving the fall migration, a period of high mortality (Owen & Black, 1989; Francis *et al.*, 1992; Menu *et al.*, 2005). Although they did not examine feeding conditions on the breeding grounds, Clausen & Clausen (2013) reported an increasing phenological mismatch between timing of spring migration and the onset of spring on the breeding grounds of light-bellied brent geese (*Branta bernicla hrota*) in Svalbard, which

they related to a low productivity (% of juveniles in autumn flocks) in recent years. In addition, size of goslings at fledging is correlated to their final adult size (Cooch *et al.*, 1991; Sedinger *et al.*, 1995), which is in turn related to their fecundity (Sedinger *et al.*, 1995).

Gosling growth was also related to spring and summer AO, although the sign of the effect changed from positive in the spring to negative in the summer. This global index appeared to be a better predictor of gosling mass and size at fledgling than the temperature index calculated from a local weather station, which suggests that AO may succeed at capturing a wider range of climatic conditions on the breeding grounds than local measurements (Hallett *et al.*, 2004). Negative AO values are associated with warm temperatures at our study site (JISAO, 2004). Thus, a positive relationship between gosling growth and spring AO supports the idea that warm and dry conditions cause plant phenology to accelerate in spring, leading to an increased mismatch between hatching and plant nutritive quality. The effect of the AO was reversed later in the summer (i.e. negative relationship between gosling growth and summer AO) presumably because cold summer temperatures (and increased rainfall) negatively impact young during the brood-rearing period, either due to increased thermoregulatory costs (Renaud, 1999), reduced foraging time due to a greater need for brooding (Fortin *et al.*, 2000) or a reduced late summer growth of their forage plants. Therefore, conditions that will maximize gosling growth appear to be cool spring temperatures and relatively late snow melt to ensure a
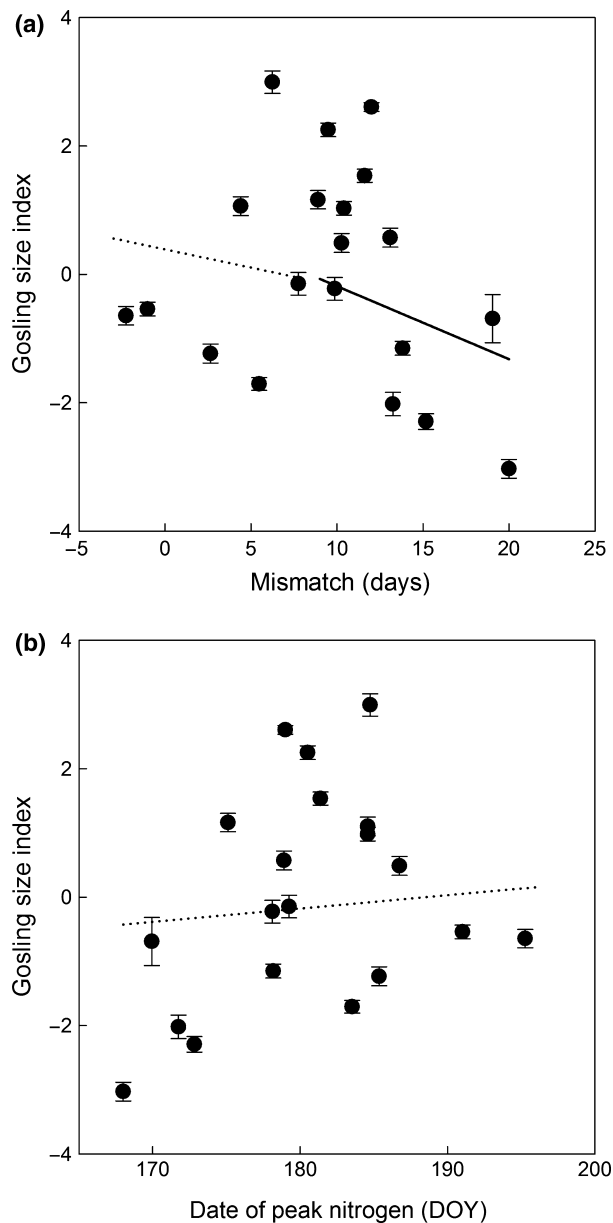
Fig. 5 Relationships between body size of goslings adjusted at 35 days and (a) mismatch between median hatch date and date of peak nitrogen concentration in plants and (b) date of peak nitrogen concentration in plants (after controlling for climate effects) on Bylot Island, NU, from 1991 to 2010. Body size index was obtained from the principal component score of head, culmen and tarsus length measurements. Dotted lines represent nonsignificant relationships (confidence interval did not exclude 0). Analyses were carried out on individual gosling measurements, but mean annual values with SE are shown to illustrate the fit of the model. Dates are in day of the year.

good synchrony between hatch and plant nutritive quality, combined with warm temperatures and dry conditions during brood-rearing to reduce energy expenditure and maximize food intake. However,

populations breeding at different latitudes may be affected differently as gosling growth in sub-Arctic snow geese, which have a shorter migration and a longer growing season, appears to be favoured by warm spring and cool summers, an opposite situation to ours (Aubry *et al.*, 2013).

Density-dependent effects on growth of young

Warm springs with early snow melt can have a positive effect on breeding propensity and success in geese (Reed *et al.*, 2004; Dickey *et al.*, 2008), and as such, spring climatic conditions are often correlated with brood density. When controlling for climatic conditions, we found no evidence of density-dependent effects on gosling size or mass in this study, which contrasts with the results obtained in a study on sub-Arctic-nesting Canada geese (*Branta canadensis*; Brook *et al.*, 2015). However, goose grazing pressure on the brood-rearing areas at this site is intense and has led to habitat degradation (Jefferies *et al.*, 2006; Kotanen & Abraham, 2013), which may explain this result.

Many populations of Arctic-nesting geese in North America have shown an exponential growth over the past 60 years and have overgrazed their habitat (Ali-sauskas *et al.*, 2011; Peterson *et al.*, 2013). However, the greater snow goose population has been relatively stable over the past 2 decades (Reed & Calvert, 2007) and has remained below the carrying capacity of its Arctic habitat (Massé *et al.*, 2001). Even though grazing by greater snow geese can reduce the standing crop in wetlands (Gauthier *et al.*, 1995; Valéry *et al.*, 2010), this impact has lessened in recent years (Gauthier *et al.*, 2013). Therefore, this could explain why we could not find density-dependent effect on gosling growth, contrary to what has been found in other goose populations (Aubry *et al.*, 2013; Brook *et al.*, 2015).

Climate change and mismatch

Arctic warming is expected to continue at a faster pace than the rest of the planet and temperature should increase by 3–5 °C at the end of the century (IPCC, 2013). This range of warming has already been shown to advance the phenology of plants and to reduce the quality of forage for Arctic herbivores (Post *et al.*, 2008; Doiron *et al.*, 2014). Unless herbivores are able to advance their phenology to keep up with such important changes in their breeding environment, they are likely to become increasingly mismatched with the period of high-quality food on the breeding grounds, and our study shows how this could have negative consequences for individuals. Although climate warming may increase total plant production and prolong the

summer season, this may not be sufficient to offset the risk of hatching well after the peak in nitrogen concentration, as food quality is low at the end of the summer (Manseau & Gauthier, 1993). Geese, like other long-distance migrants, appear to have a limited ability to track interannual variations in spring phenology on their breeding ground, which is likely to impede their capacity to adapt to increases in spring temperature in the wake of rapid global warming.

The phenomenon of trophic mismatch is widespread and has been shown to have negative impacts on species in multiple biomes (Visser *et al.*, 1998; Winder & Schindler, 2004; Lane *et al.*, 2012; Plard *et al.*, 2014; Brook *et al.*, 2015). However, its impacts may be amplified in Arctic systems due to the high seasonality of resources, the short breeding seasons and the intensity of climate warming in these regions, as has been shown in Arctic-nesting shorebirds (McKinnon *et al.*, 2012) and migratory caribou (Post & Forchhammer, 2008; Post *et al.*, 2008). Moreover, complex interactions with climate at a large spatial scale may have important consequences in Arctic ecosystems. For instance, accelerated decline in sea ice has led to temporal changes in the availability of prey for seabirds (Gaston *et al.*, 2009), but this rapid decline may also affect terrestrial herbivores. Indeed, Kerby & Post (2013) have shown that Arctic sea ice loss has contributed to the ongoing advance in plant phenology in West Greenland and thus to the decline of caribou reproductive success via trophic mismatch.

Our study provides additional evidence that trophic mismatch could have important consequences on the population dynamics of long-distance migrants by affecting the quality of their food supply. This adds to the growing body of evidence that some of the most severe impacts of climate warming on Arctic species may be indirect, through disruptions of the synchrony in the phenology of species at different trophic levels (Miller-Rushing *et al.*, 2010). This emphasizes the importance of taking a multispecies food web approach when examining the consequences of environmental change on organisms. In order to fully understand how climate change may affect long-distance migrants, it will be useful to track these species during their entire annual cycle (van Oudenhove *et al.*, 2014). By examining how changes in climate on stopover sites and on wintering grounds influences the timing of migration, we could gain a better understanding of which specific constraints are preventing migratory birds from adjusting to the rapid warming on their breeding grounds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relationships between maximum nitrogen biomass and (a) summer temperature and (b) summer AO (Arctic Oscillation) on Bylot Island, NU from 1991 to 2010.

Table S1. Results of the principal component analyses (PCA) of four temperature variables during Spring and Summer on Bylot Island, Nunavut, Canada.

Table S2. Correlation coefficients (Pearson's r values) among the climatic, plant nitrogen (N), and goose density variables on Bylot Island, Nunavut, Canada.

Table S3. Results of the principal component analysis (PCA) of three body size measurements (culmen, head and tarsus length) of goslings captured on Bylot Island, Nunavut, Canada.

Table S4. Most parsimonious models explaining variation in gosling body mass at 35 days on Bylot Island, NU in 1991, 1993, 1995, 1996 and 2006–2010 (9 years).

Table S5. Most parsimonious models explaining variation in gosling body size index at 35 days on Bylot Island, NU in 1991, 1993, 1995, 1996 and 2006–2010 (9 years).