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LETTER

Environmental change reduces body condition, but not population growth, in a high-arctic herbivore

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Abstract

Environmental change influences fitness-related traits and demographic rates, which in herbivores are often linked to resource-driven variation in body condition. Coupled body condition-demographic responses may therefore be important for herbivore population dynamics in fluctuating environments, such as the Arctic. We applied a transient Life-Table Response Experiment ('transient-LTRE') to demographic data from Svalbard barnacle geese (*Branta leucopsis*), to quantify their population-dynamic responses to changes in body mass. We partitioned contributions from direct and delayed demographic and body condition-mediated processes to variation in population growth. Declines in body condition (1980–2017), which positively affected reproduction and fledgling survival, had negligible consequences for population growth. Instead, population growth rates were largely reproduction-driven, in part through positive responses to rapidly advancing spring phenology. The virtual lack of body condition-mediated effects indicates that herbivore population dynamics may be more resilient to changing body condition than previously expected, with implications for their persistence under environmental change.

Keywords

Arctic, barnacle goose, climate change, integral projection models, life table response experiments, population dynamics, trait-mediated and modified effects, transient LTRE.

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INTRODUCTION

Fluctuations in fitness-related traits and population size are jointly affected by environmental stochasticity and density dependence (Lande *et al*., 2003; Sæther *et al*., 2016). Body condition, often measured as proxies, for example body mass or mass/tarsus ratio (Schamber *et al*., 2009), is a key fitness-related trait, reflecting energy reserves available to survive, grow and reproduce (Labocha and Hayes, 2012). Individual body condition is constantly responding to weather and density-dependent processes, as they influence food availability and energy expenditure (Sæther, 1997; Parker *et al*., 2009). Particularly in herbivores, this can directly influence reproduction and survival (Festa-Bianchet *et al*., 1997; Sæther, 1997; Post and Stenseth, 1999). Short-term effects of weather and density can also lead to cohort effects on body condition, which, in turn, can have lasting impacts on reproduction (Albon *et al*., 1987; Choudhury *et al*., 1996) and population size (Beckerman *et al*., 2002). Simultaneous changes in body condition and vital rates occur when both respond to variation in weather or density (Parmesan, 2006), with potentially complex population-growth consequences (Post *et al*., 1997; Ozgul *et al*., 2010). However, this coupling remains largely unexplored. Linking changes in fitness-related traits to variation in population growth is particularly complex when environment-trait-demography associations vary temporally (e.g. seasonally, Paniw *et al*., 2019b) or among life-history components (e.g. Douhard *et al*., 2013).

Arctic environments are seasonal and stochastic. Consequently, Arctic herbivores are exposed to variable resource availability, causing annual fluctuations in body condition and population size (Forchhammer *et al*., 2002; Couturier *et al*., 2008; Albon *et al*., 2017). Weather patterns are being modified by climate change (Scheffer *et al*., 2001), which is occurring most rapidly in the Arctic (Serreze and Barry, 2011). Accordingly, climate change effects on body condition (Albon *et al*., 2017), reproduction (Post and Forchhammer, 2008; Layton-Matthews *et al*., 2020), survival (Aubry *et al*., 2013) and population size (Forchhammer *et al*., 2002; Albon *et al*., 2017) have been documented in Arctic herbivores. However, climate effects on fitness-related traits and demographic rates do not act independently, and relatively little is known about the linkages among them due to the challenge of quantifying these – often complex – relationships (McLean *et al*., 2016; Visser *et al*., 2016; Jenouvrier *et al*., 2018). Additionally, traits can influence environment-demography relationships via two mechanisms: trait-mediating (Ozgul *et al*., 2010; Plard *et al*., 2015; Albon *et al*., 2017) or trait-modifying effects (Herfindal *et al*., 2006; Harrison *et al*., 2013). A mediating trait effect *explains* a relationship between environmental conditions and vital rates, for example temperature affects body condition, which in turn affects survival, whereas a modifying effect requires a body condition-temperature interaction effect on survival.

Since body condition is so influential on life-history processes in Arctic herbivores, we could expect large population-level responses to changes in this trait (Albon *et al*., 2017). However, changes in fitness-related traits do not necessarily affect population growth (McLean *et al*., 2020), since three conditions must be met for trait-mediated effects on population growth to arise; (1) the trait must fluctuate at the relevant life-history stage for a given, potentially age-specific, demographic rate, (2) changes in the trait must influence the demographic rate and (3) the population growth rate must, in turn, be influenced by variation in the demographic rate. If any conditions are not met, then no pathway exists from trait variation to population growth variation (Jenouvrier *et al.*, 2018).

Populations are constantly being perturbed by short-term, temporal variation in the environment (Bierzychudek, 1999; Clutton–Brock & Coulson 2002). This can lead to 'transient population dynamics' (Hastings, 2004; Koons *et al.*, 2005; Ezard *et al.*, 2010), as fluctuating environments cause changes in underlying population structure (e.g. age structure, Koons *et al.*, 2016) or trait distributions (e.g. body mass, Ozgul *et al.*, 2010). Changes in population structure can have delayed, transient effects on future population growth, especially when there is substantial variation in the vital rates of different classes of individuals (Beckerman *et al.*, 2002; De Roos *et al.*, 2003; Hansen *et al.*, 2019). If poor conditions reduce cohort body condition, vital rates can be affected for several subsequent years through delayed effects, mediated by early-life body condition (e.g. Albon *et al.*, 1987). Recent extensions of matrix (MPM) and integral (IPM) projection models have attempted to quantify population-growth consequences of such delayed ('lagged') effects (Koons *et al.*, 2005; Kuss *et al.*, 2008). Transient life-table response experiments (transient-LTREs) partition variance in the realised population growth rate into contributions from demographic rates. Furthermore, they can be used to separate temporal variation in λ into direct demographic effects versus delayed effects from transient changes in population structure/trait distributions (e.g. cohort effects), thereby explicitly incorporating past environments (Maldonado-Chaparro et al. 2018).

We explored how a substantial change in body condition contributed to variation in population growth in a high-arctic herbivore, the barnacle goose (*Branta leucopsis*). We analysed female mark-recapture and body mass data (1990–2017) to quantify environmental and density effects on survival, reproduction, growth and fledgling body mass. We used the regression models to construct an environmentally driven, stochastic IPM (Rees and Ellner, 2009; Metcalf *et al.*, 2015). Using a recently developed transient-LTRE (Maldonado-Chaparro et al. 2018), we decomposed variation in the realised population growth rate (λ_t) into vital rate contributions through demographic and trait-mediated pathways, separated into direct and delayed effects. This methodology revealed that variation in population growth was largely reproduction-driven, through direct and delayed effects (i.e. changes in age structure), whereas body condition-mediated pathways contributed negligibly to population growth. Thus, herbivore populations appear more resilient to substantial changes in body condition than anticipated, with implications for their persistence under future environmental change.

MATERIAL AND METHODS

Study species

Arctic geese are migratory capital breeders, relying, to some extent, on accumulated body reserves for reproduction (Jönsson, 1997; Hahn *et al.*, 2011). Therefore, an individual's body condition prior to the breeding season affects their reproductive success (Ankney and MacInnes, 1978; Ebbinge and Spaans, 1995). Svalbard barnacle geese overwinter in Scotland, UK (55° N, 3.30° W). They fly to Svalbard for breeding in summer, stopping over in spring along the coast of mainland Norway. The study population breeds close to Ny-Ålesund, western Spitsbergen (78°55' N, 11°56' E). Geese arrive at the end of May and nest on islands in the fjord, Kongsfjorden. Hatching occurs from late June. Families leave the nesting islands to forage thereafter, until offspring fledge at the end of August and geese migrate back to Scotland by October.

Demographic data

All analyses were female-based. Over the main study period (mark–recapture period: 1990–2017), 1669 females were caught in July-August and ringed with unique colour and metal identification bands. Recapture data were based on daily observations of ringed individuals around Ny-Ålesund during the foraging period from late June to August ($n_{obs} = 7280$). Some years were lacking recapture or body mass data (see Appendix S1 for annual sample sizes). We assessed reproduction based on observations of sexually mature adults with fledged offspring, at the beginning of August. We attributed individuals to two age classes: individuals ringed in their first year of life as 'fledglings' (*fl*) and older individuals as 'adults' (*ad*) – a pooled age class of up to 28 years old. Body mass was measured during a catch (n_{mass}/n_{total}: $fl = 691/712$, $ad = 2123/6568$). We analysed body mass, rather than other body condition proxies, since body mass is a reliable measure of condition in geese (Schmutz, 1993; Lindholm *et al.*, 1994).

Analytical approach

First, we fitted (generalised) linear mixed-effects models ((G) LMMs) to describe fledgling body mass (C_0), growth (i.e. change in body mass from t to $t + 1$, G), overwinter survival (ϕ) and reproduction: the probability of reproducing (R) and fledged brood size (*fec*). For each model, we quantified effects of age class, body mass and covariates, using model selection. Based on the best-approximating models (see Appendix S3 for more details), we constructed an IPM to model temporal dynamics of population size and body mass distribution. We decomposed variation in the population growth rate (λ_t), using a transient-LTRE, into direct effects of demographic rates versus indirect effects through fluctuations in age class structure and body mass distribution. Contributions were further decomposed into variation from environmental and density covariates versus random effects.

Regression models

We fitted an LMM to fledgling body mass data, to model the mean and distribution of fledgling body masses (C_0), including catch date as a predictor since gosling growth exhibited a seasonal trend (Appendix S2). We also fitted an LMM to body mass data of both age classes (fledglings and adults), describing body mass-dependent growth between years, due to ontogeny and phenotypic plasticity (*G*). To estimate apparent survival (ϕ), we modelled mark-recapture data with a Cormack-Jolly-Seber framework using the *RMark* interface (Laake, 2013) for program MARK (White and Burnham, 1999). We modelled detection probabilities with a fixed year effect. We fitted GLMMs to reproductive data and modelled reproduction as two response parameters. *R* describes the annual reproduction probability that is whether or not a female had at least one fledgling (0/1), fitted as a binomial response. Fledged brood size (*fec*) describes the number of fledglings per mother, fitted as a Poisson response. We included observations from 2 year-olds onwards (age of sexual maturity, Forslund and Larsson, 1992; Fjelldal *et al.*, 2020) in the reproductive models, and only successfully reproducing individuals ($R = 1$) in the model of *fec*. We fitted all (G)LMM's with year as a random effect using the package *lme4* in R (Bates *et al.*, 2015).

Using these regression models, we identified the most parsimonious model including effects of age class, body mass, density and environmental covariates (see below, *Covariates*) on C_0, G, R, fec and ϕ, using Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson, 2002). For the survival model in RMark, we imputed missing adult body mass observations using linear interpolation between two observations of an individual. We detrended body mass for model selection of G and C_0, to avoid spurious correlations caused by declining trends. We detrended body mass data against year by calculating the least-squares fit of a straight line and subtracting the resulting function from the data. A set of candidate models were fitted for each rate including all possible subsets of covariates and interactions between age class, body mass and covariates (global models shown in Appendix S3, Table S1). If competing models had ΔAICc <2, we considered the one with the least parameters as most parsimonious. Finally, since RMark does not allow for estimation of year and age-specific random effects, we fitted the most parsimonious model of survival rates including covariates (based on model selection in RMark), in a Bayesian framework to model age class- and year-specific random effects, and with year-specific detection probabilities. We implemented Markov Chain Monte Carlo (MCMC) simulations in JAGS via the *rjags* package (Plummer, 2013), assuming annual variation in survival originated from a random process with zero mean and age class-specific deviations (see Schaub *et al.*, 2013; Layton-Matthews *et al.*, 2019 for details). All priors were non-informative however, missing body mass observations were imputed by drawing from a normal distribution, where priors were set at the age class-specific mean body mass and variance (Gimenez *et al.*, 2006). While the Bayesian framework allows for estimation of age- and year-specific random effects, imputing missing body mass data can lead to under-estimation of individual heterogeneity (McCarthy and Masters, 2005).

Covariates

In addition to body mass, we included covariates reflecting weather and population density over the annual cycle, and predator abundance effects on barnacle goose demography (Layton-Matthews *et al.*, 2020) in the regression models of reproduction (*R*, *fec*), survival (ϕ), growth (*G*) and fledgling body mass (C_0). From the overwintering grounds at Solway Firth, Scotland (*win,* i.e. winter: October$_t$–March$_{t+1}$), we included annual mean winter temperature (T_{win}) and total flyway population counts (N_{win}). From the spring staging grounds at Helgeland, (*spr*, i.e. spring: April–May), we included spring precipitation (P_{spr}) using data from the Vega weather station (65°38′ N, 11°52′ E). Climate covariates from the breeding grounds in Svalbard (*sum,* i.e. summer) included temperature (mid-June–mid-July, T_{sum}) and precipitation (mid-July–mid-August, P_{sum}). Additionally, the date of spring onset (SO_{sum}) describes the onset of snowmelt and plant-growth onset at the breeding grounds, and is the (ordinal) day when the 10-day smoothed daily temperature crossed 0°C and remained above for at least 10 days (Le Moullec *et al.*, 2019). We also included estimated adult population size in Kongsfjorden (*Nsum*, Layton-Matthews *et al.*, 2019), and the proportion of occupied known dens as an index of Arctic fox (*Vulpes lagopus*) abundance (fox_{sum}), since predation by Arctic foxes affects pre-fledging survival (Fuglei *et al.*, 2003; Layton-Matthews *et al.*, 2020). More details on covariates are found in Layton-Matthews *et al.* (2020).

Stochastic integral projection model

We constructed a stochastic IPM, describing temporal dynamics of population size and body mass distribution, $n(m, t)$, of fledglings (*fl*) and adults (*ad*), following the life cycle in Fig. 1. The growth kernel, $G^{(t)}(m', m)$, describes the probability density function of body masses m' in August in year $t + 1$ of an individual of body mass m in year t. Annual age-class specific survival, $\Phi^{(t)}(m, a)$, describes the probability of an individual, of age class *a* (*fl* or *ad*) and body mass *m*, at year *t*, surviving to year $t + 1$. $P_{ad}^{(t)}(m',m)$ and $P_{fl}^{(t)}(m',m)$ represent survival-growth kernels for adults and fledglings describing how individuals of body mass *m* at time *t*, survive and grow to reach mass *m'* at $t + 1$, given by:

$$P_{a}^{(t)}(m',m) = \Phi^{(t)}(m,a)G^{(t)}(m',m) \text{ for } a = \textit{fledglings} \text{ or } \textit{adults} \quad (1)$$

Annual reproduction probability, $R^{(t)}(m)$, describes the probability of a >1-year-old female of body mass *m* producing at least one fledgling at $t + 1$, given she survives. Fledged brood size, $fec^{(t)}$, describes the number of fledglings per mother at $t + 1$, conditional on reproduction. Fledgling body mass kernel, $C_0^{(t)}(m')$, describes the probability distribution of fledgling body masses in August at $t + 1$. This was assumed to be independent of mother body mass, since a pedigree was not available. $F_{ad}^{(t)}(m', m)$ is the reproduction kernel, describing the density of fledglings of body mass *m'* that adults of body mass, *m,* can contribute to the population at year $t + 1$;

$$F_{ad}(m',m) = \Phi^{(t)}(m,ad)R^{(t)}(m)fec^{(t)}C_0^{(t)}(m')/2 \quad (2)$$

Reproduction was divided by 2 since the model was female based. The structure of the IPM was:

$$n_{fl}(m', t+1) = \int_{L}^{U} F_{ad}^{(t)}(m',m)n_{ad}(m, t)dm \quad (3)$$

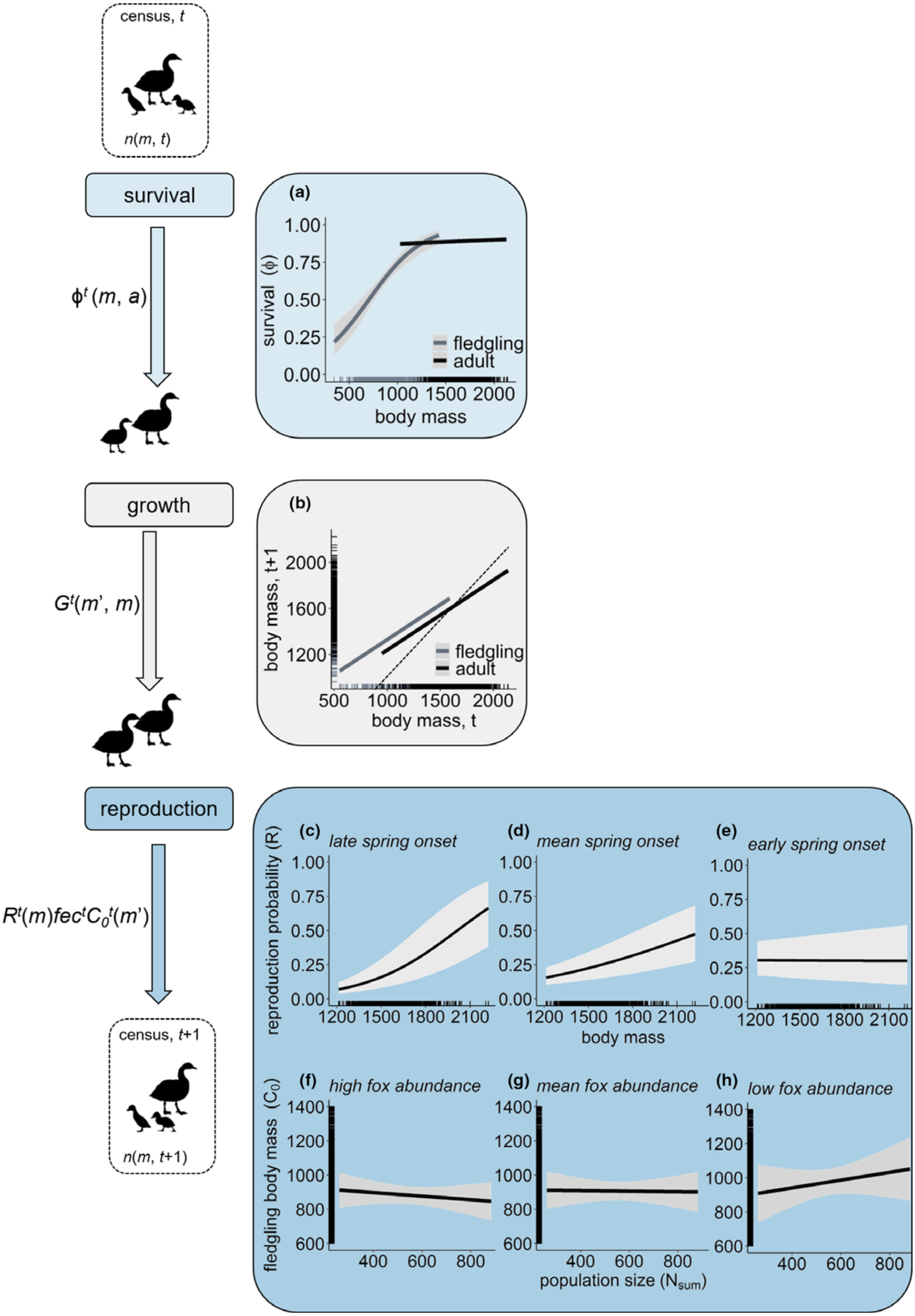

Figure 1 Life cycle of barnacle geese based on a post-breeding census (i.e. breeding occurs just before a census). Individuals in age class *a* must survive with a body mass(m)-dependent probability ($\phi(m, a)$) and grow to the next year ($G(m', m)$) in order to reproduce ($R(m)$, *fec*) and contribute fledglings of body mass ($C_0(m')$) to the population. Model predictions of body mass effects at *t* on; (a) fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, (b) body mass at $t + 1$ (dashed line = 1:1 slope), reproduction probability (R) of adult females at the (c) 20th quantile, (d) mean and (e) 80th quantile of the date of spring onset (SO_{sum}). Effects of adult population size at the breeding grounds (N_{sum}) on fledgling body mass (C_0) at the (f) 20th, (g) mean and (h) 80th quantile of Arctic fox abundance (fox_{sum})

$$
\begin{aligned}
n_{ad}(m', \mathrm{t}+1) &= \int_L^U \mathrm{P}_{ad}^{(t)}(m',m)n_{ad}(m, t)dm \\
&+ \int_L^U P_{fl}^{(t)}(m',m)n_{fl}(m,t)dm
\end{aligned}
\tag{4}
$$

We simulated stochastic population dynamics, assuming density-independent population growth, and employed a two-step Monte Carlo resampling approach (Metcalf *et al.*, 2015). Details of the simulation and Monte Carlo resampling approach can be found in Appendix S4.

Transient life table response experiment

Life table response experiments (LTREs) decompose variance in a demographic response metric (typically, population growth rate) into contributions arising from spatial or temporal variation in vital rates. LTREs have become a standard approach to study population-level responses to environmental factors, with fixed, random and regression designs routinely applied to plant and animal populations (Caswell, 1989). Here, rather than studying asymptotic population growth rates, with the assumption that the population is always close to its stable structure, we decomposed variance in the realised population growth rate at time $t(\lambda_t)$. Specifically, we used an extension of the Monte Carlo regression-random LTRE (Rees and Ellner, 2009), to incorporate transient fluctuations in age structure and body mass distribution (Maldonado-Chaparro et al. 2018). We included lagged parameter effects in the model of λ_t, to quantify delayed effects of parameters (i.e. parameter i at time t, $\theta_{i,t}$), acting through changes in age structure or body mass distribution. We compared variance decompositions of λ_t assuming either linear (linear model, LM) or nonlinear (generalised additive model, GAM) dependencies of λ_t. Following Maldonado-Chaparro et al. (2018), we decomposed variance in $\log(\lambda_t)$. We compared the R^2 of LMs and GAMs and incorporated delayed effects with increasing numbers of (year) lags to capture the impact of fluctuating stage-structure and body condition. We also tested whether interaction effects between parameters (pairwise smooths for GAMs) contributed to substantial variation in $\log(\lambda_t)$. We considered a model of $\log(\lambda_t)$ to be a better fit when the amount of variance explained increased by at least 1%. To summarise relative contributions of each term, we calculated scaled contributions by dividing the (co)variance contribution from a given term by the total variance in $\log(\lambda_t)$ (Maldonado-Chaparro et al. 2018).

Vital rate contributions were further partitioned into variation from modelled covariate effects versus random effects. In this case, (net) contributions of covariates to λ_t depended on; (1) temporal covariances among covariates, (2) their effect size on $\theta_{i,t}$ and (3) the sensitivity of λ_t to $\theta_{i,t}$. We assumed linear dependencies of λ_t on $\theta_{i,t}$ for the environmental decomposition. In the IPM, trait-mediated effects could contribute to intercept variation in each function, whereas trait-modified effects would cause variation in the slope describing the relationship between body mass and a function. Consequently, we decomposed variation in $\log(\lambda_t)$ at three hierarchical levels; (1) overall contributions from C_0, G, R, fec and ϕ, (2) modelled environment versus random effects and (3) slope versus intercept variation.

RESULTS

Body mass and life-history processes

The most parsimonious model of overwinter survival (ϕ) included an interaction effect between age class and body mass, with a much stronger positive effect on fledglings than adults (Fig. 1a), and additive effects of overwintering population size (N_{win}, negative effect) and winter temperature (T_{win}, positive effect) (Table 1). The best growth model (G), estimating body mass at year $t + 1$, included a positive effect of body mass at t (Fig. 1b). The best model of reproduction probability (i.e. of an adult female producing fledglings, R) included spring precipitation (positive effect, P_{spr}) and date of spring onset (negative effect, SO_{sum}), and an interaction effect between mother body mass and SO_{sum}, with a strong, positive body mass effect in late springs and no effect in early springs (Fig. 1c–e). For fledged brood size (fec), the best model included negative effects of Arctic fox abundance (fox_{sum}) and summer precipitation (P_{sum}). The best model of fledgling body mass (C_0) included an interaction effect of fox_{sum} and adult population density at the breeding grounds (N_{sum}), where N_{sum} tended to have a negative effect only at high fox abundance (Fig. 1f-h). Further description of the model selection and associated tables (Tables S3, 1-3.5) can be found in Appendix S3.

Over the study period, average cohort body mass declined significantly ($\text{slope} = -8.3$ g per cohort, $\text{SE} = 0.8$ g, $p < 0.001$). Interannual changes in body mass were relatively small for adults, but larger for fledglings (Fig. 2).

Transient LTRE

The mean stochastic population growth rate λ was 1.07 (95% confidence intervals: 0.77, 1.59) (Appendix S4,^{t} Fig. S1), which was similar to the observed growth rate (1.05; 0.65, 1.53). The stable body mass-age class distribution reflected the bimodal distribution of fledgling and adult body mass (Appendix S4, Fig. S2). 94% of the variation in λ_t was explained by the main effects of the functions, including a one-year time lag, with a transient linear LTRE (LM-LTRE), which increased to 98% with a generalised additive model (GAM-LTRE). The only pairwise smooth (interaction between parameters) explaining more than 1% variance was between the intercept and slope terms of reproduction probability (R) – since SO_{sum} was a predictor in both terms. Parameter effects with more than a 1-year lag explained <1% of the variance in λ_t.

Sensitivity surfaces were estimated using the GAM-LTRE for $\log(\lambda_t)$, illustrating the influence of each function through direct (Fig. 3a) and delayed effects (Fig. 3b). Direct effects of variation operating through reproduction probability (R) were larger than survival (ϕ) or fledged brood size (fec). λ_t was sensitive to variation through survival rates, in particular adult survival (Fig. 3a). Direct effects of variation through changes in growth and fledgling body mass are not included in Fig. 3a since changes in body mass only affect λ the following year

Table 1 Linear predictors for best-approximating regression models of each function, with mean parameter estimates, used to parameterise the integral projection model (IPM)

IPM function	Model	Best-fitting regression model
Survival	$\mathrm{logit}(\phi_{fl,\ ad})$	$-2.67 + 4.32\boldsymbol{a} + 0.004\boldsymbol{m} - 0.003\boldsymbol{a{:}m} + 0.22\boldsymbol{T_{win}} - 0.21\boldsymbol{N_{win}}$
Growth	G	$648.50 + 0.60\boldsymbol{m}$
Fledgling body mass	C_0	$-3357.40 + 19.46\boldsymbol{c} - 2.37\boldsymbol{fox_{sum}} - 46.30\boldsymbol{N_{sum}} - 7.70\boldsymbol{fox_{sum}{:}N_{sum}}$
Reproductive rate	$\mathrm{logit}(R)$	$-3.76 + 0.002\boldsymbol{m} + 0.86\boldsymbol{P_{spr}} - 3.52\boldsymbol{SO_{sum}} + 0.002z{:}\boldsymbol{SO_{sum}}$
Fledged brood size	$\log(fec)$	$0.77 - 0.16\boldsymbol{fox_{sum}} - 0.10\boldsymbol{P_{sum}}$

Functions included the covariates; winter temperature ($\boldsymbol{T_{win}}$) and overwinter population size ($\boldsymbol{N_{win}}$) in Scotland, Arctic fox abundance ($\boldsymbol{fox_{sum}}$), adult population size ($\boldsymbol{N_{sum}}$), the date of spring onset ($\boldsymbol{SO_{sum}}$) and summer precipitation ($\boldsymbol{P_{sum}}$) at the breeding grounds on Svalbard and spring precipitation at the spring stopover site at Helgeland ($\boldsymbol{P_{spr}}$). $\boldsymbol{a}$ is a dummy variable equal to 0 for fledglings (*fl*) and 1 for adults (*ad*), $\boldsymbol{m}$ refers to body mass and $\boldsymbol{c}$ to catch date.

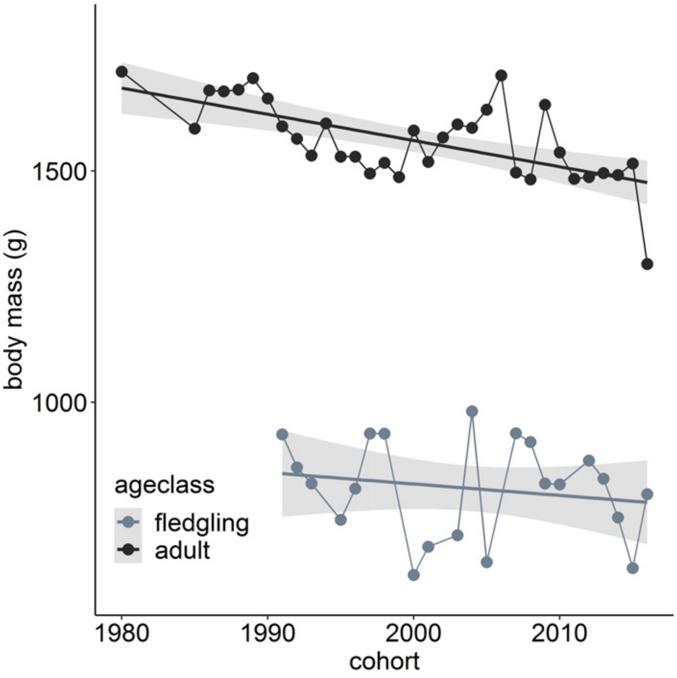

Figure 2 Temporal trends in average cohort adult (black, 1980–2016) and annual fledgling (grey, 1991-2016) body mass. Slope (bold line) with 95% confidence intervals (shading) were calculated based on a linear regression, with year as an explanatory variable

(i.e. delayed effects). Population growth was insensitive to delayed effects (Fig. 3b) through G and C_0 (i.e. trait-mediated effects). The sensitivity of λ_t to delayed effects (i.e. at t-1) through R and fec reflects how increased reproduction in a given year had a negative impact the following year, via a shift in the age structure towards a larger proportion of non-reproductive individuals.

Vital rate contributions, arising from variances and covariances in $\log(\lambda_t)$, were separated into direct and delayed effects. The largest vital rate contribution to variation in $\log(\lambda_t)$ stemmed from variation in reproductive probability, R, (81%, Fig. 4), through both direct effects (69%) and delayed effects (12%, i.e. changes in age structure). Remaining variation was explained by direct and delayed contributions from variation in fledged brood size (fec, 7%), adult survival (ϕ_{ad}, total contribution = 6%) and fledgling survival (ϕ_{fl}, 3%). Changes in body mass acting through fledgling body mass and growth functions (i.e. trait-mediated effects) made negligible contributions to variance in λ_t (0.04% through G and 0.5% through C_0).

Reproductive probability and fledged brood size were negatively correlated with adult survival (ϕ_{ad}) and their covariances led to a negative contribution to the variance in log (λ_t) of −7%. Both reproductive parameters (R and fec) and survival parameters (ϕ_{fl} and ϕ_{ad}) positively covaried, each contributing 3% to log (λ_t).

Vital rate contributions were further decomposed into variance explained by environment and density covariates versus random effects. 58% of the variation in log (λ_t), acting through reproduction probability (R), was attributed to modelled covariates (Fig. 4). Precipitation at the spring stopover site (P_{spr}) contributed to 26% of the variation, while date of spring onset at the breeding grounds (SO_{sum}) contributed 16% through intercept and slope variance. 59% of the variation in log (λ_t) that was attributed to adult survival (ϕ_{ad}) was explained by temperature (T_{win}) and population size (N_{win}) at the wintering grounds, accounting for 1% and 2% of the overall variation in log (λ_t). In contrast, < 1% of the variation in fledgling survival was attributed to T_{win} and N_{win} although these covariates explained 95% of the positive covariation between fledgling and adult survival, leading to a positive contribution of 1% to variation in log (λ_t) (Fig. 4). Finally, 65% of the variation in log (λ_t) through fledged brood size (fec) was explained by Arctic fox abundance and summer precipitation, each contributing 3% to variation in $\log(\lambda_t)$.

DISCUSSION

Coupled trait-demography responses to environmental change may be key to understand and predict short- and long-term population dynamics, especially in Arctic herbivores. Using a transient-LTRE, we quantified population growth responses to a substantial, temporal decline in body mass (body condition proxy) in an Arctic goose population, caused by degradation of the Arctic breeding grounds. For such trait-mediated effects on population growth to arise, three conditions must be met; the trait must fluctuate, changes in the trait must influence the demographic rate and population growth must be influenced by variation in the demographic rate (Table 2). Here, trends and interannual fluctuations in body condition (Fig. 2) did not incur population growth responses because all three conditions were not met. Although body condition at

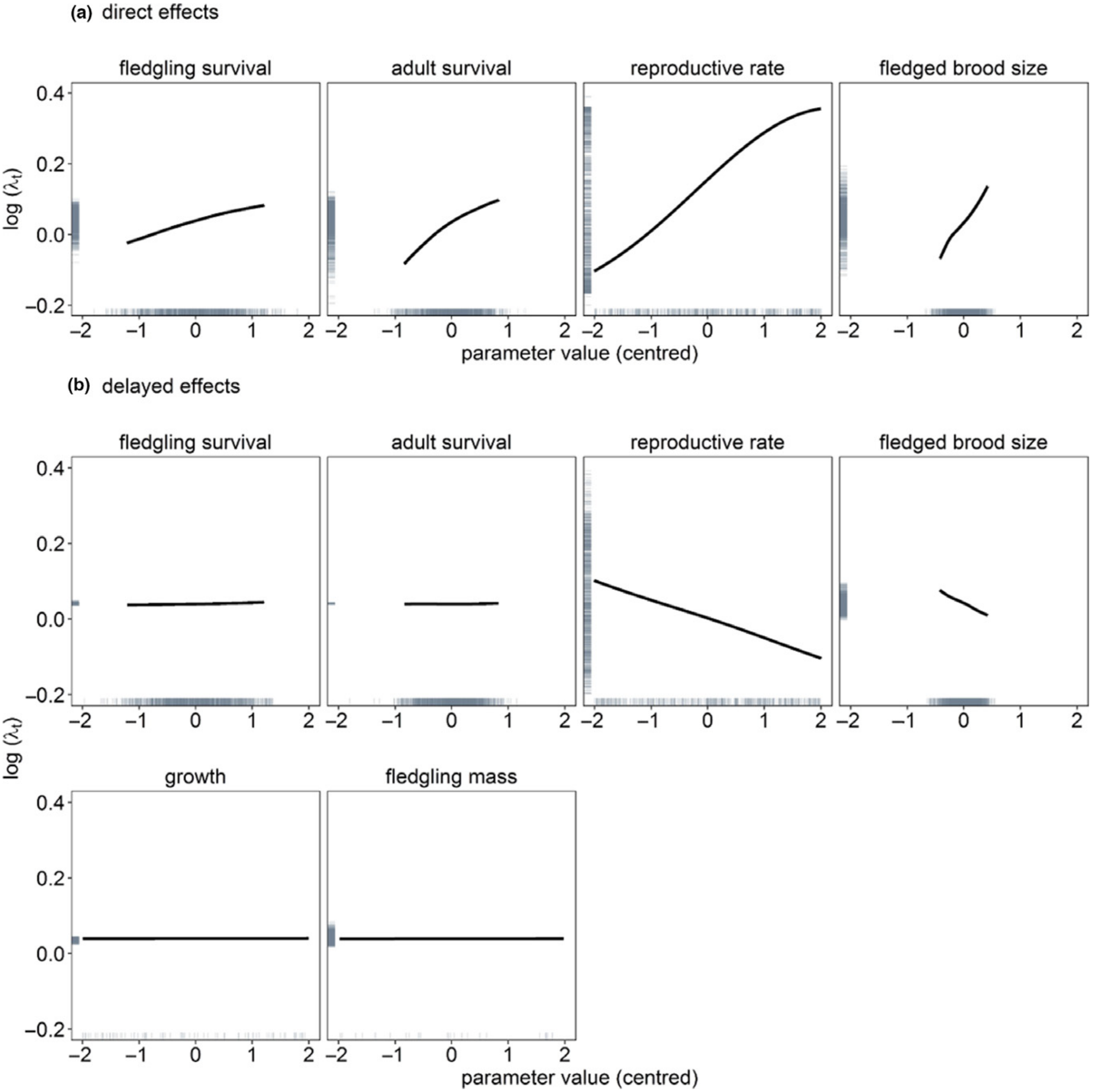

Figure 3 Sensitivity surfaces illustrating the effects of fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, reproductive rate (R), fledged brood size (fec), growth (G) and fledgling body mass (C_0) on the population growth rate, $\log(\lambda_t)$. Contributions from each vital rate parameter were separated into (a) direct and (b) delayed contributions, that is parameter effects at t and t-1 respectively, on $\log(\lambda_t)$. The x-axis and y-axis rugs show distributions of parameters (centred values) and $\log(\lambda_t)$ respectively

fledging strongly affected fledgling survival (Fig. 1a), population growth was insensitive to fledgling survival (Fig. 3a). Conversely, population growth was sensitive to changes in adult survival, which was insensitive to body condition. Variation in population growth was instead largely explained by direct and delayed effects operating through reproduction, in part shaped by annual variation in spring onset (Fig. 4) and only weakly influenced by adult body mass.

Both resident and migrant Arctic herbivores are exposed to variable weather conditions, resulting in variation in body condition and population size (Festa-Bianchet *et al.*, 1997; Sæther, 1997). Although weather and density effects on body condition are well documented in herbivores, whether these effects extend to variation in population growth remains largely unanswered. Goose populations have expanded across the Arctic, as a result of increasing population size caused by hunting bans and agricultural change at overwintering grounds (Madsen and Cracknell, 1999; Fox and Madsen, 2017). Density-dependent processes associated with overgrazing by geese have degraded Arctic breeding grounds, leading to declining body condition in Arctic geese (Cooch *et al.*, 1991b; Loonen *et al.*, 1997; Reed and Plante, 1997; Larsson

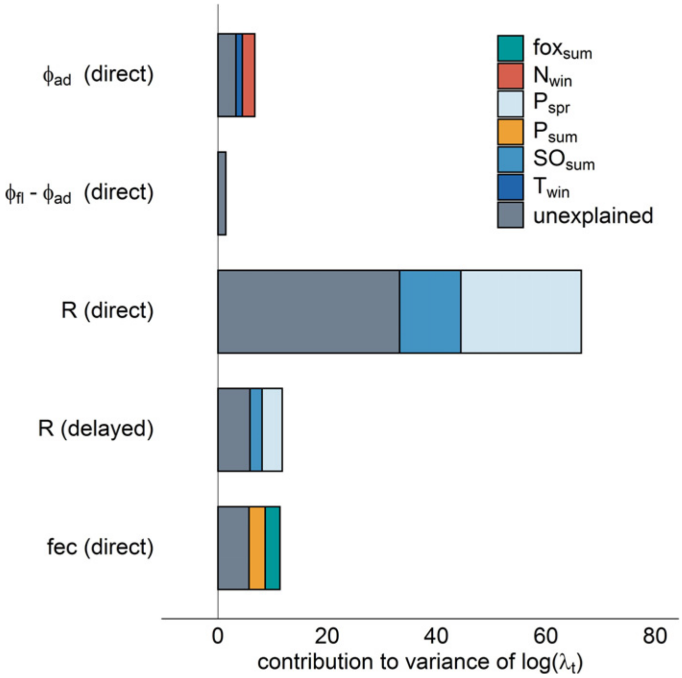

Figure 4 Percentage contributions of the largest demographic contributions (through adult survival, ϕ_{ad}, fledgling survival, ϕ_{fl}, reproduction probability, *R* and fledged brood size, *fec*) to variance in the population growth rate, log(λ_t). Contributions were decomposed into direct and delayed variances and covariances. Colours represent contributions from modelled covariates versus unexplained variation (random effects)

Table 2 Summary of which conditions for body mass-mediated effects on the population growth rate (for each demographic rate) were met or not (✓ = condition met). All conditions need to be met for body mass-mediated effects on the population growth rate to arise.

Condition	Fledgling survival (ϕ_{fl})	Adult survival (ϕ_{ad})	Reproduction probability (*R*)	Fledged brood size (*fec*)
Body mass fluctuates at relevant stage	✓			
Body mass change influences demographic rate	✓		✓	
Variation in demographic rate influences λ		✓	✓	✓

et al., 1998). Cohort adult body condition in the study population declined by 10% from 1980 to 2017. We documented density dependence in fledgling body condition at high Arctic fox abundance, that is the main predator of goslings and, occasionally, adults (Fuglei *et al.*, 2003). Foxes therefore influenced geese through lethal effects on fledged brood size (*fec*) and non-lethal effects on fledgling body condition, through density-dependent restrictions on their ability to utilise available foraging areas (Loonen *et al.*, 1998).

Despite the temporal decline in (cohort) adult body condition, interannual fluctuations in adult body condition were small. Fledgling body condition exhibited more interannual variation, likely a result of strong resource dependence during growth (Cooch *et al.*, 1991a; Lindholm *et al.*, 1994). Body condition, in turn, positively influenced survival and reproduction. The reserves which first-year-geese accumulate at the breeding grounds affect survival during migration (Owen and Black, 1989; Menu *et al.*, 2005), reflected in the strong positive effect of fledgling body condition on first-year survival found here. Adult survival, however, was largely unaffected by body condition.

Several studies have stressed the potential importance of coupled trait-demography responses in predicting population persistence under environmental change (Ozgul *et al.*, 2009, 2010; Plard *et al.*, 2014; Jenouvrier *et al.*, 2018). Direct evidence of this is scarce, however, and several studies have indicated that trait changes may lead to more limited population-level responses than expected (Wilson and Arcese, 2003; Maldonado-Chaparro et al. 2018; McLean *et al.*, 2020). Here, despite the potential for coupled body condition-demography responses, changes in Arctic goose body condition did not incur population-level responses through trait-mediated effects. Over the study period, body condition declined and positively influenced demographic rates. However, these trends and interannual fluctuations in body condition did not translate into effects on population growth because all three conditions required for trait-mediated pathways to arise were not met for any age class-specific demographic rate (Table 2). Although body mass influenced fledging survival, variance in fledgling survival contributed negligibly to population growth, since fledglings represent a small fraction of the population. In contrast, population growth was sensitive to changes in adult survival, but this vital rate was insensitive to body condition. Likewise, population growth was also highly sensitive to changes in reproductive rate, which was only weakly influenced by adult body condition. Importantly, despite adult body condition showing a pronounced long-term decline, interannual fluctuations were limited. Resulting in a lack of trait-mediated effects on population growth rates through reproduction. Nevertheless, further changes in body condition could have large effects on population growth, operating through reproduction, and long-term, delayed consequences of changes in fledgling mass (i.e. 'silver spoon effects', Madsen and Shine, 2000) could also be important. However, in our study population no significant effect of fledgling mass was found on adult mass, adult survival or reproduction (i.e. no evidence for silver spoon effects).

According to the demographic buffering hypothesis, variability in population growth reduces fitness (Tuljapurkar, 1982), leading to selection for reduced variance (Gaillard and Yoccoz, 2003; Jongejans *et al.*, 2010). In long-lived species, individuals may, when resources are scarce, increase/maintain their survival by limiting investment in reproduction. Buffering of population growth against trait-mediated variation may occur via such mechanisms. However, in cases where body condition influences adult survival we might expect population-level responses (e.g. Pigeon *et al.*, 2017). Therefore, the magnitude of population-level responses to body condition likely depends on species' life history and the way in which individuals utilise resources (i.e. capital versus income breeding). In capital breeders, where body condition is important for reproductive success, we could therefore expect strong effects on population growth, given substantial annual variation in adult body mass and reproduction. However, both in barnacle geese (this study) and in other capital breeders (e.g. van Benthem *et al.*, 2017; Maldonado-Chaparro et al. 2018), changes in body condition did not induce population-level responses, likely as a result of low variation due to demographic buffering. A lack of population-level effects of body condition was also observed in income-breeding passerine birds (McLean *et al.*, 2020), indicating that the capital-income breeding dichotomy cannot predict species variation in trait-mediated effects on population growth. However, in several partially capital-breeding ungulate species, changes in body condition did elicit population-level responses (e.g. Soay Sheep, Pelletier *et al.*, 2007; Svalbard reindeer, Albon *et al.*, 2017; bighorn sheep, Pigeon *et al.*, 2017). In these cases, annual fluctuations in body condition were relatively large and body condition influenced adult survival as well as recruitment. This suggests that population-level responses requires body condition to induce variation in vital rates with a large impact on population growth (e.g. adult survival). Body condition may also be less constrained (and more variable) in ungulates, compared to, for example, migratory birds, where individuals carry reserves over long distances (Owen and Black, 1991).

Individual heterogeneity in body condition, which often becomes increasingly important under poor environmental conditions (Barbraud and Weimerskirch, 2005), can also help to understand the lack of trait-mediated effects on population growth. In geese, larger individuals tend to gain better access to resources due to dominance behaviour, and thus reproduce better (Stahl *et al.*, 2001). Within-year, rather than among-year, variation in body condition may thus be relevant also in understanding density-dependent effects, that is through intra-specific competition. Such discrepancies between individual- and population-level responses to trait variation have been documented previously (Reed *et al.*, 2013). Although we assumed density-independent population growth in the IPM, density dependence may explain some of the unexplained variation in population growth. Either through effects on survival, as found here and in previous studies (Layton-Matthews *et al.*, 2020), but also on reproduction since density-dependent effects have been found in previous studies (Layton-Matthews *et al.*, 2019). An additional limitation was the lack of a pedigree, that is mother body mass was not included as a predictor of fledgling body mass. If body mass is heritable, as found in barnacle geese in the Baltic (Larsson and Forslund, 1992), this would lead to a positive correlation between adult growth and fledgling mass, influencing fledgling survival. However, since variation in fledgling survival made a small contribution to population growth, the population-level impact should also be minimal.

Quantifying demographic and associated trait responses to climate change is necessary for a mechanistic and predictive understanding of population-level consequences (Jenouvrier, 2013; Paniw et al. 2019a). Arctic warming is advancing snow melt, with widespread effects on plant phenology, while rising summer temperatures are influencing plant productivity (Bjorkman *et al.*, 2020). For migrating Arctic geese, spring phenology at the breeding grounds also dictates when nesting sites become snow-free as well as the onset of plant growth: both important determinants of breeding success (Reed *et al.*, 2004; Madsen *et al.*, 2007). Positive effects of earlier spring onset on fledgling production has previously been attributed to females laying bigger clutches with improved hatching success (Layton-Matthews *et al.*, 2020). Advancing spring phenology could therefore benefit reproduction and population growth, which appear unhampered by the temporal decline in body condition (since effects of body condition on reproduction diminish with earlier springs). However, neither reproductive parameter exhibited positive temporal trends (Appendix S6), likely due to contrasting direct versus indirect climate change effects, as the number of Arctic foxes – and thus gosling predation rates – are generally increasing (Layton-Matthews *et al.*, 2020; unpublished data, E. Fuglei).

In capital breeders, such as Arctic geese, the accumulation of body stores is beneficial in unpredictable environments, and this strategy is typical at higher latitudes (Varpe *et al.*, 2009; Sainmont *et al.*, 2014). Storing resources along their flyway allows geese to initiate reproduction without immediate food access (Klaassen *et al.*, 2017). Consequently, several reproductive stages depend on fat reserves (Bêty *et al.*, 2003; Guillemain *et al.*, 2008; Aubry *et al.*, 2013), reflected here in the positive relationship between body condition and reproduction. Here, spring onset operated through a trait-modified effect on reproduction, where heavier individuals were more likely to reproduce than lighter ones under poor (delayed) spring conditions, since they have more ‘capital’ to initiate reproduction. While in earlier springs (i.e. typically in more recent years), with excess nesting sites and food resources, benefits of accumulating fat reserves were reduced and the influence of body condition on reproduction was weaker. Further advanced springs due to climate change could tip the balance in favour of accumulating fewer resources for reproduction, potentially relaxing selection on body condition if individuals gain a survival advantage by requiring fewer fat reserves for migration (Larsson *et al.*, 1998).

Overall, population dynamics of Arctic migratory geese appear unaffected by the decline in body condition, thus far. Buffering population growth against changes in body condition, which is essential for survival and reproduction in Arctic herbivores, has clear implications for their resilience to future environmental change. However, as the Arctic continues to change, further declines in body condition could potentially have big effects on population growth, via trait-mediated effects through reproduction.

This work emphasises the importance of holistic approaches capturing pathways from environmental variation to individual and population-level responses. Even when environmental change substantially alters trait distributions that are correlated with vital rates, we cannot assume this will have population-level consequences.

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Data supporting the results are archived in Dryad data repository: https://doi.org/10.5061/dryad.9p8cz8wdv.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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