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Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming

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Abstract

Climate change is most rapid in the Arctic, posing both benefits and challenges for migratory herbivores. However, population-dynamic responses to climate change are generally difficult to predict, due to concurrent changes in other trophic levels. Migratory species are also exposed to contrasting climate trends and density regimes over the annual cycle. Thus, determining how climate change impacts their population dynamics requires an understanding of how weather directly or indirectly (through trophic interactions and carryover effects) affects reproduction and survival across migratory stages, while accounting for density dependence. Here, we analyse the overall implications of climate change for a local non-hunted population of high-arctic Svalbard barnacle geese, *Branta leucopsis*, using 28 years of individual-based data. By identifying the main drivers of reproductive stages (egg production, hatching and fledging) and age-specific survival rates, we quantify their impact on population growth. Recent climate change in Svalbard enhanced egg production and hatching success through positive effects of advanced spring onset (snow melt) and warmer summers (i.e. earlier vegetation green-up) respectively. Contrastingly, there was a strong temporal decline in fledging probability due to increased local abundance of the Arctic fox, the main predator. While weather during the non-breeding season influenced geese through a positive effect of temperature (UK wintering grounds) on adult survival and a positive carryover effect of rainfall (spring stopover site in Norway) on egg production, these covariates showed no temporal trends. However, density-dependent effects occurred throughout the annual cycle, and the steadily increasing total flyway population size caused negative trends in overwinter survival and carryover effects on egg production. The combination of density-dependent processes and direct and indirect climate change effects across life history stages appeared to stabilize local population size. Our study emphasizes the need for holistic approaches when studying population-dynamic responses to global change in migratory species.

1 | INTRODUCTION

The climate is changing most rapidly in the Arctic, as a consequence of Arctic amplification (Arft et al., 1999; Serreze & Barry, 2011). Climate change has disrupted abiotic and biotic processes (Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Post et al., 2009) and thereby the population dynamics of many species, through altered snowpack characteristics (Hansen et al., 2019), phenological mismatch (Clausen & Clausen, 2013; Doiron, Gauthier, & Lévesque, 2015; Post & Forchhammer, 2008) and changes in vegetation productivity ('Arctic greening') and structure (e.g. Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017).

Earlier snow melt has long been recognized as one of the prevailing indicators of Arctic climate change (Foster, 1989). The snow-free season, and thus the growing season, is extremely short at high latitudes. Earlier snow melt may therefore benefit Arctic wildlife populations (Gareth, 2004) and especially herbivores. Warmer temperatures and advancing springs have increased plant productivity (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Jensen et al., 2008), providing more food for both resident and migratory herbivores (Hill & Henry, 2011; Van der Wal & Stien, 2014) and potentially increasing reproduction, survival and, in turn, population sizes. Positive trends associated with climate change have been observed in some Arctic herbivore populations (Albon et al., 2017; Forchhammer et al., 2008; Morrissette, Bêty, Gauthier, Reed, & Lefebvre, 2010). However, there has been little evidence for a general pattern of increase (Post et al., 2009). This may be partly explained by negative effects of 'trophic mismatch' (i.e. poor timing of reproduction in relation to resource peaks), limiting the potential benefits of earlier and warmer springs (Clausen & Clausen, 2013; Doiron et al., 2015; Saino et al., 2011), as well as changing winter conditions (Forchhammer, Post, Stenseth, & Boertmann, 2002; Hansen et al., 2019, 2013; Kohler & Aanes, 2004). In addition, climate change effects may be indirect through other species in the Arctic community, across trophic levels (Forchhammer et al., 2008; Hansen et al., 2013; Post et al., 2009), causing changes in 'bottom-up' and 'top-down' processes (Forchhammer et al., 2002; Gauthier, Bêty, Giroux, & Rochefort, 2004). Arctic herbivore populations are often strongly influenced by bottom-up processes (i.e. food resource availability; Barrio et al., 2016). Fluctuations in Arctic fox, *Vulpes lagopus*, abundance also has distinct top-down effects on population dynamics, affecting reproductive success in geese (Gauthier et al., 2004; Loonen, Tombre, & Mehlum, 1998) and survival in voles (Ehrich et al., 2017) and lemmings (Angerbjorn, Tannerfeldt, & Erlinge, 1999).

The Arctic is the breeding grounds for many migratory species (Dickey, Gauthier, & Cadieux, 2008). Long-distance migrants (such as those breeding in the high Arctic) occupy widely separated habitats across the annual cycle and are therefore exposed to different climate regimes and trends, and also potentially contrasting density-dependent effects (Both, Bouwhuis, Lessells, & Visser, 2006; Hüppop & Winkel, 2006; van Oudenhove, Gauthier, & Lebreton, 2014). The time spent on migration often accounts for a large proportion of the annual cycle and individuals are dependent on food resources at each migratory stage. Therefore, climate-induced changes in plant productivity and the timing of the plant growing season can be a major source of mortality (Newton, 2006, 2007). Consequently, migrants may be particularly vulnerable to climate change (Robinson et al., 2009), as possibly reflected in the declining trends reported for several long-distance migrant populations (Both et al., 2006). However, predicting their population responses to climate change clearly depends on understanding how climate—and other drivers—affects vital rates at each stage of the annual cycle. Reproductive success in Arctic nesting geese is largely determined by weather conditions during the breeding season (Bêty, Gauthier, & Giroux, 2003; Madsen et al., 2007; Prop & de Vries, 1993), but conditions earlier in the annual cycle may also affect individuals at later stages via carryover effects. Especially in capital breeders, nutrients accumulated prior to the breeding season determine body condition and thereby affect reproduction (Inger et al., 2010; Sedinger, Schamber, Ward, Nicolai, & Conant, 2011). Carryover effects can contribute substantially to reproductive success and thus population dynamics in Arctic goose populations (Marra, Hobson, & Holmes, 1998; Norris, 2005).

The extent to which climate change affects population dynamics also depends on a species' life history (Sæther et al., 2013). In long-lived species such as geese, population growth is often more sensitive to variation in survival than reproduction. Consequently, reproduction may be more susceptible to environmental variability (Gaillard & Yoccoz, 2003; Morris & Doak, 2004) and therefore climate change (Koons, Gunnarsson, Schmutz, & Rotella, 2014). It is also crucial to account for intrinsic regulation of population dynamics through density dependence when studying the effects of environmental variation (Sæther et al., 2006). Total flyway population sizes have been steadily increasing in most European Arctic-nesting goose populations, largely due to hunting bans since the 1950s (Fox & Madsen, 2017) and shifts in agriculture (Fox & Abraham, 2017). This increase has resulted in range expansion across the Arctic (Kondratyev, Zaynagutdinova, & Kruckenberg, 2013; Owen & Norderhaug, 1977). While local density-dependent effects on reproduction have been found in some populations (Bruggeman, Swem, Andersen, Kennedy, & Nigro, 2015; Ebbinge, Heesterbeek, Ens, & Goedhart, 2002; Layton-Matthews et al., 2019), density dependence may also be expected to affect survival at other stages in the annual cycle (Frederiksen & Bregnballe, 2000).

Arctic nesting geese play a key trophic role both as herbivores (Bazely & Jefferies, 1989; Fujita & Kameda, 2016) and prey (Bêty, Gauthier, Korpimäki, & Giroux, 2002), providing nutrient transfer within and between temperate and Arctic ecosystems (Hahn, Loonen, & Klaassen, 2011; Hessen, Tombre, van Geest, & Alfsnes, 2017). Substantial differences in local population trends of geese at their Arctic breeding grounds have been reported (Jensen et al., 2008; Lameris et al., 2018; Morrissette et al., 2010). Disentangling the drivers of these trends is key to a predictive understanding of future climate change implications. Besides the potential issue of mismatch in migratory timing with peak food abundance (Dickey et al., 2008; Kölzsch et al., 2015; Lameris et al., 2017), future climate change will likely disrupt other processes affecting reproduction and survival, for instance through trophic interactions (Ims, Jepsen, Stien, & Yoccoz, 2013). Here, we assess the contributions of climate, trophic interactions and density dependence to population dynamics of a local, non-hunted population of Svalbard barnacle geese, *Branta leucopsis*. Using individual-based mark–recapture data, we determine the main drivers of each reproductive stage (egg laying, hatching and fledging) and age class-specific survival, across their annual cycle. We quantify the contributions of direct and indirect drivers to population growth using a retrospective perturbation analysis and investigate how temporal trends in environmental variables influence population growth.

FIGURE 1 Migration route and timing of key events for Svalbard barnacle geese. Barnacle geese overwinter at Solway Firth, Scotland (blue), before travelling to western Svalbard for breeding (pink) via a stopover on the coast of mainland Norway (green). The timing of migrations and reproductive events (nesting, hatching, moulting and fledging) are shown in the outer circle (NB: failed breeders can moult earlier than shown here)

2 | MATERIALS AND METHODS

2.1 | Study population

The Svalbard barnacle goose population overwinters at Solway Firth, Scotland (UK; 55°N, 3.30°W), before flying to Svalbard for breeding in summer, with a spring stopover at Helgeland on the coast of mainland northern Norway (65°45′N, 12°E; Figure 1). Barnacle geese are close to the capital end of the capital–income breeding spectrum, investing between 23% and 88% of body stores acquired further south in egg production (Hahn et al., 2011). We studied a population breeding close to the settlement of Ny-Ålesund, northwestern Svalbard (78°55′N, 11°56′E) that arrives in late May and nests on islands in the fjord (Kongsfjorden). Hatching occurs around the 1 July (range: 19 June–19 July) and after hatching, families leave the nesting islands to forage along the coast. Offspring fledge at the end of August and individuals leave the breeding grounds in September (Figure 1). Barnacle geese typically begin breeding as 2 year olds (Forslund & Larsson, 1992; Owen, 1980).

2.2 | Data collection

Individual mark–recapture data from both sexes were collected from the nesting islands and coastal area around Ny-Ålesund (see Section 2.2). Using these data, we assessed the effects of climate, population size and predation (see Section 2.3) on three stages of reproduction (egg laying, hatching and fledging), as well as on apparent survival of fledglings (0 year old) and adults (1–28 years old). We identified the
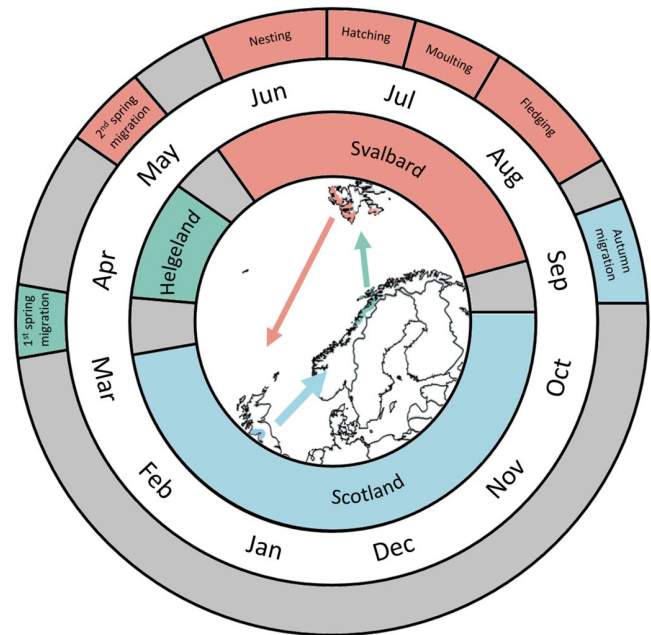
best models with covariates of reproduction using a path analysis framework and model selection (see Section 2.4) and determined the best-fitting survival model using model selection (see Section 2.5). We developed a population matrix projection model using the best-fitting models of vital rates, to quantify the contribution of covariates to population growth using a retrospective perturbation analysis (see Section 2.6).

The study area consists of two nesting islands, Storholmen and Prins Heinrichsøya, and the area close to the settlement of Ny-Ålesund, where goose families forage on tundra vegetation. The analysis was conducted on individual-based data from 1990 to 2017 (ringing of individuals began in 1989). Three thousand two hundred and ninety nests were monitored over this 28 year period. The islands were visited at 1 or 2 day intervals during the nesting period. Females with a clutch (n = 5,828) were identified and the clutch size (maximum number of eggs per nest) was recorded (n = 2,111). Data on clutch size were not recorded in the years 1994, 1997, 2000, 2002 and 2004 as the islands were not visited.

Over the study period, 3,487 individuals (goslings and older birds) have been caught around Ny-Ålesund and ringed with unique, engraved colour and metal rings, during the moulting phase in July and early August. During a catch, sex was determined by cloacal inspection. During the brood-rearing phase in July–August, twice-daily ring readings took place and whether a female had any offspring

(n = 5,872) and the number of goslings associated with the parent was recorded (n = 2,799). The maximum number of fledged goslings per female was recorded in mid-August (n = 1,976). Observational data for modelling hatching and fledging were not recorded for the year 2004. Annual sample sizes for each parameter are shown in Appendix S1.

2.3 | Covariates

We included covariates describing population size, weather and predation that could affect reproductive and survival rates over the annual cycle, for the years 1990–2017.

2.3.1 | Scotland: Wintering grounds

For the wintering period in Scotland, mean daily minimum and maximum temperature and precipitation data were taken from the Eskdalemuir weather station (55°39′N, 3°21′W), 40 km from Solway Firth, provided by the UK Meteorological Office (metoffice.gov.uk, 2018). Annual averages were calculated for the period October–March ($T_{scot,min}$, $T_{scot,max}$, P_{scot}; minimum and maximum temperatures were used since mean temperature values were not available). Svalbard flyway population size (N_{scot}), recorded at the wintering grounds in Scotland (Trinder, 2014; WWT, 2017), was included to determine whether density-dependent effects at the wintering grounds, via flyway population size, affected survival.

2.3.2 | Helgeland: Spring stopover site

For the spring stopover site at Helgeland, daily mean temperature and precipitation values for the period April–May were based on data from the Vega weather station (65°38′N, 11°52′E), within the spring range of barnacle geese. Annual means for the period April–May were calculated from the daily data ($T_{helg,am}$, $P_{helg,am}$). We also tested for an effect of the sum of positive temperatures above 6°C ($T_{helgsum6}$), since net grass growth is positive above this threshold (Prop, Black, Shimmings, & Owen, 1998). Data were obtained from the Norwegian Meteorological Institute (eklima.met.no, 2018).

2.3.3 | Svalbard: Breeding grounds

Covariates describing initial conditions at the breeding grounds (Ny-Ålesund, Svalbard) included cumulated snowfall from November to April ($snow_{sval}$; see Peeters et al., 2019) and date of spring onset (range: 13 May–21 June). Spring onset (SO_{sval}) describes the date (Julian day) at which the 10 day smoothed daily temperature crossed 0°C and remained above this threshold for at least 10 days (Le Moullec, Buchwal, van der Wal, Sandal, & Hansen, 2019). Daily mean temperature and precipitation data were used to calculate averages for mid-June to mid-July ($T_{sval,jj}$, $P_{sval,jj}$) and mid-July to mid-August ($T_{sval,ja}$, $P_{sval,ja}$). These covariates may influence conditions during hatching and fledging since mean temperature is a good predictor of plant phenology, while variation in rainfall

relates to plant growing conditions (Jia, Epstein, & Walker, 2009; Prop & Black, 1998), potentially explaining variation in reproduction via indirect effects on food resource availability. Data were taken from the manned Ny-Ålesund weather station, operated by the Norwegian Meteorological Institute. Annual estimates of adult numbers in the study population around Ny-Ålesund (i.e. a subset of the total Svalbard breeding population) were included ($N_{sval,ad}$), to test for density-dependent effects (see Layton-Matthews et al., 2019 for details). The Arctic fox is the main predator of eggs and goslings, but also adults (Eide, Stien, Prestrud, Yoccoz, & Fuglei, 2012; Fuglei, Øritsland, & Prestrud, 2003; Pedersen et al., 2018). Consequently, gosling survival can be strongly influenced by fox predation (Loonen et al., 1998; Morrissette et al., 2010). We used a measure of Arctic fox predation (fox_{sval}) around Ny-Ålesund, based on annual records of the proportion of known den sites with pup production during the summer period from 1993 to 2017 (the annual Arctic fox monitoring program of the Norwegian Polar Institute). We assumed a linear increase from zero dens with pups in 1990 to 1993, since data were not available for 1991 and 1992 (Fuglei et al., 2003).

In a post hoc analysis, we investigated the correlations between climate variables included in the best-fitting reproductive models and variables describing the timing of snow melt, the timing of plant growth onset and plant productivity. To assess whether the estimated spring onset date (SO_{sval}) was a good proxy for timing of snow melt (i.e. when nest sites become available), we regressed SO_{sval} against a measure of the timing of snow melt at Ny-Ålesund for the years 1993–2016 (Maturilli, Herber, & König-Langlo, 2015). We regressed $T_{sval,jj}$ against a measure of the onset of the plant growing season, defined as the mean (Julian) date when the pixel-specific Normalized Difference Vegetation Index (NDVI) values exceeded 70% of mid-summer NDVI (Karlsen, Anderson, Van der Wal, & Hansen, 2018; Karlsen, Elvebakk, Høgda, & Grydeland, 2014), which was available for the years 2000–2014. $P_{sval,ja}$ was regressed against average standing crop of *Poa arctica*, an important food source for barnacle geese (i.e. a proxy for food availability). Repeated measurements were taken between July and August from exclosures (to prevent grazing), as part of a long-term plant experiment at Ny-Ålesund for the years 2004–2016 (Appendix S2).

2.4 | Reproduction

Reproduction was modelled in three stages to investigate the stepwise mechanisms determining recruitment of fledglings. Egg laying (C and E) was based on data from the nesting islands and (post-)hatching (H and G) and fledging (F) were based on data from ringed individuals around Ny-Ålesund.

Two variables were used to describe the egg laying phase, C and E, where C is the proportion of nesting females observed with a clutch, and E is the number of eggs per clutch. To estimate C, data on whether a female was observed with at least one egg in the nest (0/1) were fitted as a binomially distributed response variable. To estimate E, data on the number of eggs per clutch (range:

1–9) were fitted as a normally distributed response variable. The variables H and G quantified the average gosling production per female breeder. H, hatching success, is the estimated proportion of females with at least one gosling around Ny-Ålesund. Observation data were fitted using a binomial distribution for the response. G is the expected number of goslings per successful female and data were modelled with a Poisson distribution (note that 'hatching' refers to the first observation of a female with goslings when they return from the nesting islands). F describes the proportion of goslings fledging and data were modelled with a binomial distribution. All models were fitted as (generalized) linear mixed-effects models, with female ID and year as random effects in addition to other covariates. All models were fitted using canonical link functions. Since reproductive success in barnacle geese has been shown to increase until age 5 (Black, Prop, & Larsson, 2014; Forslund & Larsson, 1992), we tested for age (class) effects in an initial analysis. We began with a model with five age classes (where the fifth class includes individuals ≥5 years old) and progressively reduced the number of classes. Akaike's information criterion adjusted for small sample sizes (AIC$_c$) was used to identify the best-fitting age model (Burnham & Anderson, 2002).

Covariates included in the candidate model set of egg laying (C and E) included $T_{scot,min}$, $T_{scot,max}$, P_{scot} and N_{scot} in Scotland, $T_{helg,am}$, $P_{helg,am}$ and $T_{helgsum6}$ at Helgeland (i.e. carryover effects) and SO$_{sval}$, snow$_{sval}$ and $N_{sval,ad}$ on Svalbard. The candidate model set of hatching (H and G) included $T_{sval,jj}$, $P_{sval,jj}$, fox$_{sval}$ and $N_{sval,ad}$ and the candidate model set of fledgling probability (F) included $T_{sval,ja}$, $P_{sval,ja}$, fox$_{sval}$ and $N_{sval,ad}$.

Confirmatory path analysis (Shipley, 2000, 2009) was used to identify the important intrinsic and extrinsic drivers of reproduction. We constructed a path diagram with all proposed links between covariates and response variables and tested the proposed independence relationships among variables using d-separation tests (Appendix S3; Shipley, 2009, 2016). To account for dependencies among reproductive stages, the response variable E was entered as a predictor in the models of the later reproductive stages H and G, and G was included in the model of F (Appendix S4.1). Best-fitting models for each of the five reproductive parameters were identified separately (C, E, H, G and F). To evaluate the best-fitting model of reproduction with covariates, we ranked models according to their AIC$_c$ and also examined whether they explained a significant amount of deviance by performing an analysis of deviance using the package 'afex' (Singmann, Bolker, & Westfall, 2015).

Means and 95% confidence intervals were calculated for all covariate effects in the best-fitting models of each response variable. (Generalized) linear mixed-effects models were modelled in R, version 3.5.0 (R Core Team, 2018) using the package 'lme4' (Bates, Mächler, Bolker, & Walker, 2014), and d-separation tests were performed using 'piecewiseSEM' (Lefcheck, 2016). All covariates were standardized, including reproductive parameters when entered as explanatory variables.

2.5 | Survival

We estimated age-specific, apparent (we could not distinguish between mortality and permanent emigration) survival rates based on mark–recapture data from Ny-Ålesund. Survival rates were estimated with a Cormack–Jolly–Seber framework, in the RMark interface (Laake, 2013) for program MARK (White & Burnham, 1999). Survival rates were modelled for two age classes, fledglings (ϕ_f) and adults (ϕ_{ad}), where ad is a pooled age class from 1 to 28 years (i.e. maximum observed age) old. Survival rates were not found to be sex specific. Detection probability was modelled as sex, but not age, specific since female philopatry is often higher than male philopatry (Black et al., 2014) and no effect of age was found in a previous analysis of this study population (Layton-Matthews et al., 2019). Accordingly, this analysis also showed that detection probabilities were higher for females (mean: 0.62; 95% confidence interval: 0.60, 0.65) than males (0.55; 0.54, 0.56). Survival was modelled from August (i.e. at the time of fledgling) until August the following year. Based on a survival model with two age classes, ϕ_f and ϕ_{ad}, we developed a candidate model set with all combinations of standardized covariates from the winter and spring locations (see Section 2.3) that were not highly correlated.

Covariates from the wintering grounds and the spring stopover site were included in the candidate model set of survival (Appendix S4.2), since substantial natural mortality occurs during migration and particularly the autumn migration when individuals fly directly from Svalbard to Scotland (Owen & Black, 1989, 1991b). Summer conditions likely influence body condition and mortality during the autumn migration, however, since we were not able to distinguish seasonal survival rates, only covariates from later stages in the annual cycle (i.e. the wintering grounds and spring stopover site) were included. Arctic fox abundance (fox$_{sval}$) was included as a potential cause of mortality during the summer prior to the census. To determine the best-fitting additive model of survival with covariates, we first ranked models according to AIC$_c$ and then performed an analysis of deviance in program MARK. After identifying the best additive model, we determined the best model with interaction effects between age class and covariates using the same approach.

To investigate the potential influence of climate change on reproduction and survival, we tested for temporal trends in the estimated vital rate parameters and covariates from the best-approximating models, by fitting linear regressions with a continuous year effect as an explanatory variable.

2.6 | Population dynamics

We constructed a 2 × 2 population projection matrix, based on a post-breeding census, corresponding to the fledgling and adult age classes. In accordance with a post-breeding census, recruitment of fledglings included adult (i.e. breeder) survival, ϕ_{ad}, since they must survive almost a full year before reproducing. The top left matrix element is zero since 1 year old birds generally do not reproduce. The reproductive rates H (which was no longer conditional on C and E), G and F were divided by 2 to calculate the number of fledglings per

female. C and E were not included, since this would inflate reproductive rates (both E and H are the expected number of offspring per female at different stages of the reproductive cycle). Consequently, covariates influencing C and E were included as effects on H instead. The resulting population projection matrix was

$$\begin{bmatrix} 0 & \dfrac{(\phi_{ad} \times H \times G \times F)}{2} \\ \phi_f & \phi_{ad} \end{bmatrix}.$$

We calculated the asymptotic population growth rate (λ) as the dominant eigenvalue of the population projection matrix, calculated at the mean value of covariates included in the best-fitting models. We accounted for uncertainty in model regression coefficients by assuming that regression coefficients arise from a multivariate normal distribution, where the coefficients and variance–covariance matrix from each model provided the means and variance–covariance matrix (Gelman & Hill, 2006). Vital rates were predicted using the regression coefficients sampled 10,000 times from the multivariate normal distribution. Population matrices were constructed with each sample of vital rates to calculate the mean population growth rate with 95% confidence intervals. Using this approach, we determined the change in λ when vital rates in the population matrix were predicted at a low value of a covariate (5th quantile) and a high value (95th quantile). This difference in λ was decomposed into vital rate contributions using a life table response experiment (LTRE), a common retrospective perturbation analysis (Caswell, 1989; Horvitz, Schemske, & Caswell, 1997). The contribution of a covariate was calculated as the product of (a) the difference in the affected vital rate between the two matrices (5th vs. 95th); and (b) the sensitivity of λ to that vital rate. Sensitivities were calculated analytically using the chain rule (Caswell, 2001). Analysis of the projection matrix was conducted in R using our own code and the 'popbio' package (Stubben & Milligan, 2007).

3 | RESULTS

3.1 | Reproduction

The best-fitting path model for reproduction included dependencies among reproductive phases (i.e. egg laying, hatching and fledging),

as well as effects of population size, climate, predation and carryover effects from the spring stopover site and wintering grounds (Figure 2). None of the response variables were found to be age dependent.

The model of clutch success (C) with the lowest AIC_c included date of spring onset (SO_{sval}), where a later onset had a negative effect (Figure 2). This model also included positive carryover effects of the average maximum daily temperature from October to March ($T_{scot,max}$) at the wintering grounds in Scotland and mean April–May precipitation at the spring stopover site at Helgeland ($P_{helg,am}$; Appendix S5.1.1). However, the difference between the lowest AIC_c model and one with only SO_{sval} was negligible ($\Delta AIC_c = 0.35$). $T_{scot,max}$ and $P_{helg,am}$ were only present in five and four of the top nine models, respectively, and did not explain a significant amount of variance, based on the analysis of deviance (Appendix S5.2). However, the difference in AIC_c with SO_{sval} and the null model was greater than 2 ($\Delta AIC_c = 2.40$). Therefore, the best-approximating model of C only included an effect of SO_{sval}.

The model of clutch size (E) with the lowest AIC_c also included a negative effect of SO_{sval}, a negative carryover effect of population size at the wintering grounds (N_{scot}) and a positive effect of $P_{helg,am}$ (Appendix S5.1.2; Figure 3a–c). SO_{sval} and $P_{helg,am}$ were present in all nine of the top models and explained a significant amount of variation (Appendix S5.2). N_{scot} was present in eight of nine of the top models and explained a significant amount of deviance ($p = .03$). The difference in the lowest AIC_c model and a model without N_{scot} was 1.64, and so the best-approximating model of E included SO_{sval}, $P_{helg,am}$ and N_{scot}.

The lowest AIC_c model of hatching success (H) included positive effects of clutch size (E), which was present in all top 10 models, and mid-June to mid-July temperature ($T_{sval,jj}$; Figure 3d). Although the next best model ($\Delta AIC_c = 1.04$) only included an effect of E, $T_{sval,jj}$ was present in four of five top models and the amount of variance it explained was close to being significant at the .05 level ($p = .08$). A negative effect of $N_{sval,ad}$ was only included in 40% of the top nine models (Appendix S5.1.3) and so the best-approximating model of H included E and $T_{sval,jj}$.

The lowest AIC_c model of the number of goslings (G) included a positive effect of E and weak negative effects of $N_{sval,ad}$ and fox_{sval}.
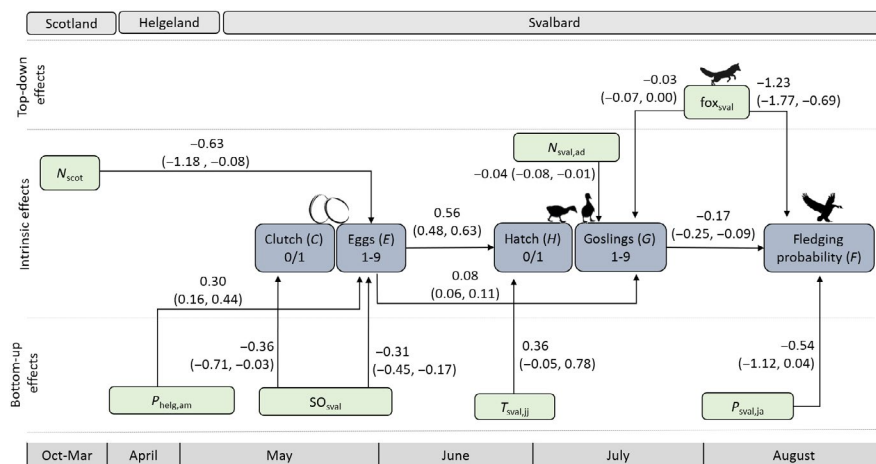

FIGURE 2 Best-fitting path model diagram for the reproductive stages, with standardized slope coefficients and associated 95% confidence intervals in brackets
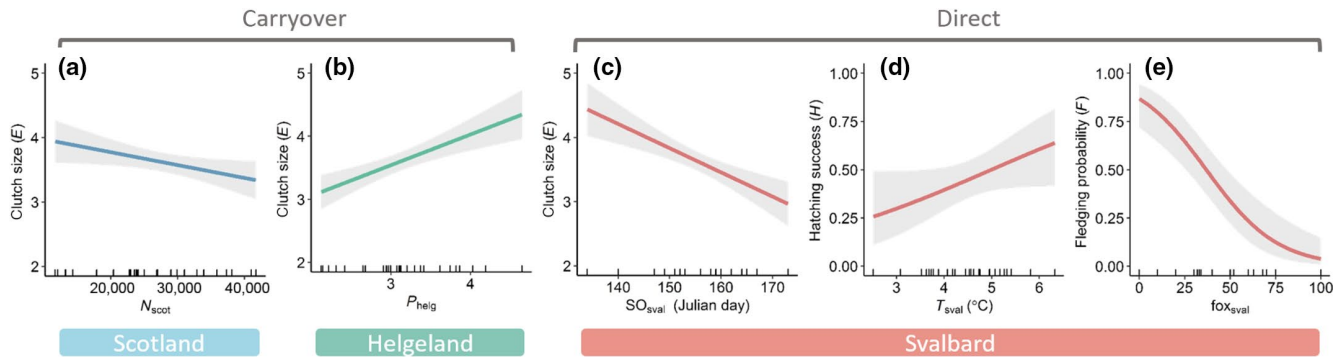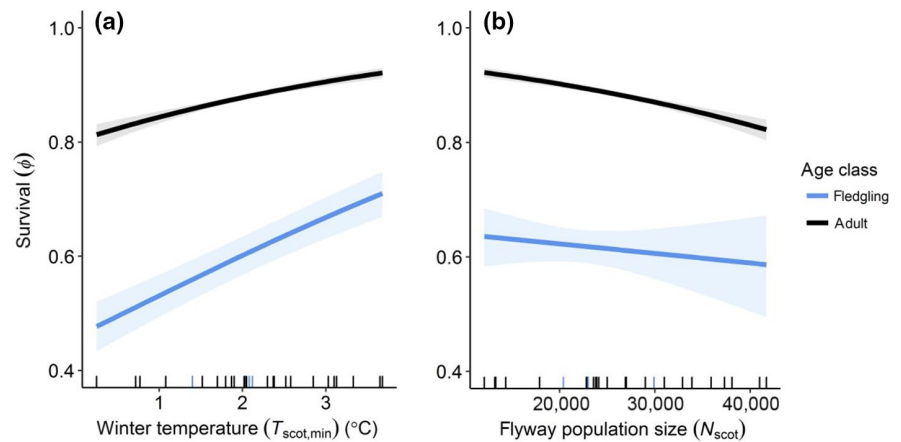
FIGURE 3 Model predictions with 95% confidence intervals, describing (a, b) the carryover effects of (a) flyway population size in Scotland (N_{scot}) and (b) spring precipitation at Helgeland ($P_{helg,am}$), and (c–e) the direct effects of (c) the onset of spring (SO_{sval}) at the Svalbard breeding grounds on clutch size (E), (d) summer temperature on Svalbard ($T_{sval,jj}$) on hatching success (H) and (e) fox abundance (fox$_{sval}$) on fledging probability (F). Data distributions are shown on the x-axis as rugs

FIGURE 4 Model predictions with 95% confidence intervals describing the effect of (a) Scotland winter temperature ($T_{scot,min}$) and (b) total flyway population size (N_{scot}) on the survival rate of fledglings (ϕ_f) and adults (ϕ_{ad}). Data distributions are shown on the x-axis as rugs

E was consistently present in all 10 of the top-ranking models, while $N_{sval,ad}$ was present in 60% and fox$_{sval}$ in 70% (Appendix S5.1.4). Both $N_{sval,ad}$ and fox$_{sval}$ were close to, but not, significant at the .05 level ($P_{Nsval,ad}$ = 0.07; $P_{foxsval}$ = 0.08). A weak positive effect of $T_{sval,jj}$ and a weak negative effect of $P_{sval,jj}$ were both present in 40% of the top 10 models. Since $N_{sval,ad}$ and fox$_{sval}$ were both consistently present in the top models and close to being significant, we considered the best-approximating model of G to include E, $N_{sval,ad}$ and fox$_{sval}$.

The lowest AIC$_c$ model of fledging probability (F) included negative effects of G, fox$_{sval}$ (Figure 3e) and mid-July to mid-August precipitation on Svalbard ($P_{sval,ja}$; Appendix S5.1.5). G was included in all eight top-ranking models, fox$_{sval}$ was included in seven of eight and the amount of variance both covariates explained was significant ($p < .01$). Although the second-best model did not include $P_{sval,ja}$ (ΔAIC_c = 1.29) and $P_{sval,ja}$ did not explain a significant amount of variation at the .05 significance level ($p = .07$), this variable was included in three of four top-ranked models with a consistently strong negative effect. Consequently, we considered the best-approximating model of F to include G, fox$_{sval}$ and $P_{sval,ja}$.

There was a strong positive correlation between SO_{sval} and the timing of snow melt, where the standardized correlation coefficient was 0.65 (0.24, 1.07) (R^2 = 0.31), and a negative correlation between mid-June to mid-July temperature ($T_{sval,jj}$) and the date of plant growth onset (−0.78;

−1.15, −0.41; R^2 = 0.61). $T_{sval,jj}$ was also strongly negatively correlated (−0.89; −1.06, −0.72) with the date at which temperature sum on Svalbard reached 180°C (plant growing degree-days, GDD) (Van Wijk et al., 2012). There was also a negative correlation (−0.64; −1.06, −0.21; R^2 = 0.49) between mid-July to mid-August precipitation and the standing crop of the grass *P. arctica*, an important food species for barnacle geese (Appendix S2).

3.2 | Survival

Apparent survival was lower for fledglings (0.62; confidence interval: 0.59, 0.65) than for adults (0.83; 0.80, 0.84). The best-fitting model of survival included a positive effect of minimum winter temperature in Scotland ($T_{scot,min}$) and a negative effect of flyway population size in Scotland (N_{scot}; Figure 4a), as well as weak negative effects of fox abundance at Ny-Ålesund (fox$_{sval}$) and precipitation at Helgeland ($P_{helg,aprmay}$) and a positive effect of the sum of positive temperatures above 6°C at Helgeland ($T_{helg,sum6}$; Appendix S5.3). However, only $T_{scot,min}$ and N_{scot} explained a significant amount of variance based on the analysis of deviance (Appendix S5.4). A model with an interaction effect between age class and N_{scot} was a better fit than the best additive model (ΔAIC_c = 4.18) since N_{scot} had a more negative effect on adults than fledglings (Figure 4b; Appendix S5.5).

3.3 | Temporal trends

Date of spring onset (SO_{sval}) became earlier over the study period (−0.05; −0.10, −0.01) and was a predictor of clutch success and clutch size, which also exhibited positive temporal trends ($C = 0.05$; 0.01, 0.11, $E = 0.06$; 0.00, 0.11; Figure 5a). Mid-June to mid-July temperature ($T_{sval,jj}$) exhibited a positive temporal trend (0.06; 0.03, 0.11), as did hatching success, H, (0.07; 0.01, 0.12), while the number of goslings (G) did not show a trend (0.01; −0.06, 0.07). There was a tendency for a trend of increasing fox abundance (0.03; −0.02, 0.08), while the probability of fledging (F) declined dramatically over the study period (−0.06; −0.12, −0.01). Total flyway population size (N_{scot}) showed a consistent increase over the study period (0.12; 0.11, 0.14), while both fledgling, ϕ_f, and adult, ϕ_{ad}, survival exhibited significant

declines (Figure 5b). Other covariates did not exhibit a clear trend; summer precipitation in Svalbard, $P_{sval,ja}$, (0.00; −0.05; 0.05), mean minimum temperature in Scotland, $T_{scot,min}$ (0.00; −0.04, 0.05; Appendix S6), and adult population size in Svalbard, $N_{sval,ad}$ (0.03; −0.02, 0.08; Figure 5c).

3.4 | Population dynamics

The mean asymptotic population growth rate (λ) was 1.05 (0.92, 1.17) based on vital rate estimates with covariates at their observed mean values. Best-fitting models of vital rates with covariates used in this analysis are shown in Appendix S4.3. λ was more sensitive to adult survival than to reproductive rates (H, G, F) and fledgling survival (Appendix S7).
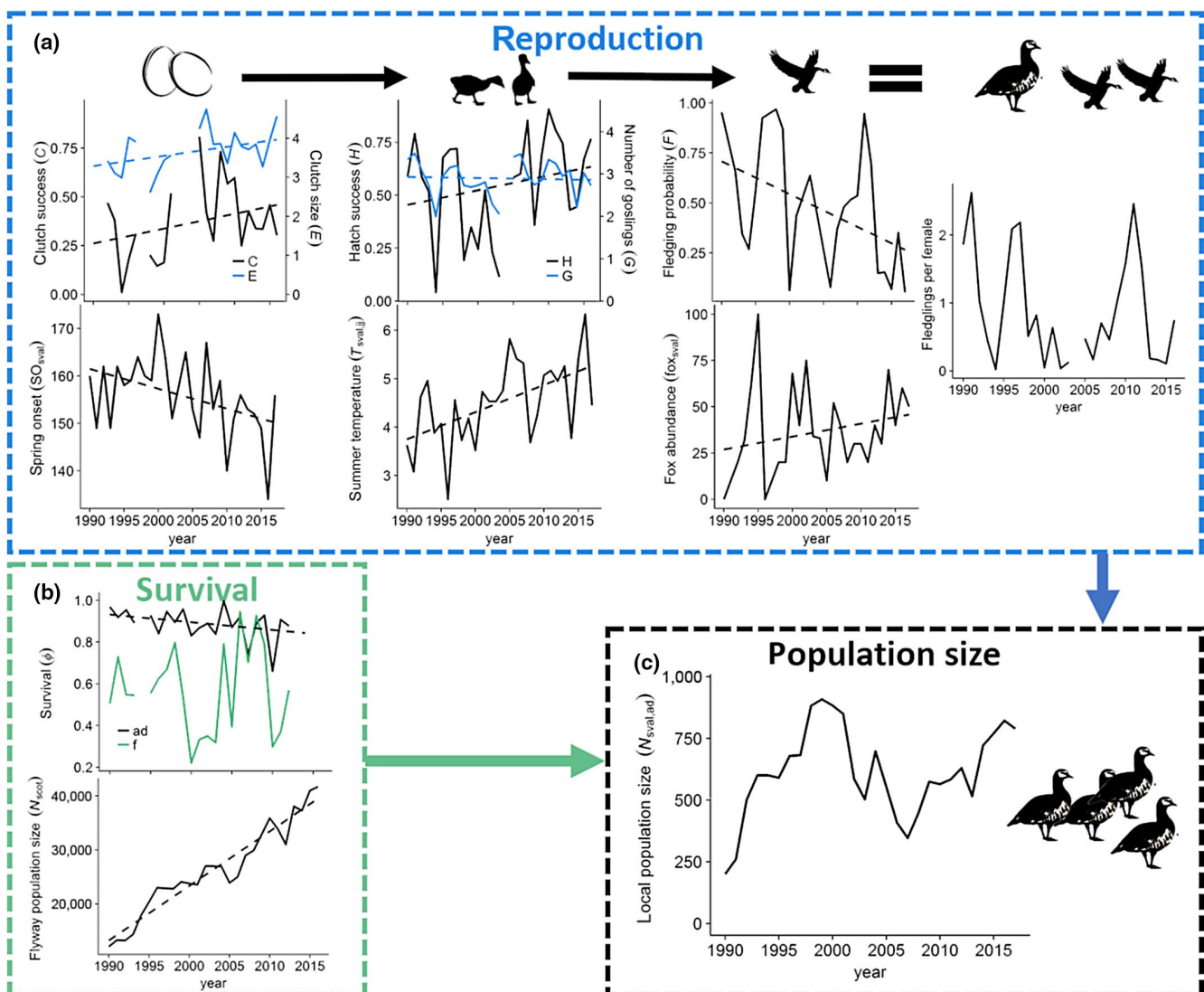

FIGURE 5 Trends in barnacle geese parameters and associated explanatory variables. For reproduction, from left to right: (a) clutch success (C) and clutch size (E) and the predictor spring onset (SO_{sval}); hatch success (H) and the predictor mid-June to mid-July temperature ($T_{sval,jj}$); fledging probability (F) and the predictor Arctic fox abundance (fox_{sval}); and number of fledglings per female ($H \times G \times F$). For survival (b), apparent survival rates of fledglings (ϕ_f) and adults (ϕ_{ad}; based on a model with additive age class and time effects) and the predictor counts of total flyway population size in Scotland (N_{scot}). For local population size (c), annual estimates of adult numbers in the local Svalbard breeding population ($N_{sval,ad}$)

TABLE 1 Mean population growth rates estimated at the 5th (λ_{5th}) and at the 95th (λ_{95th}) quantile of important covariates affecting one or more vital rates. 95% credible intervals are shown in brackets

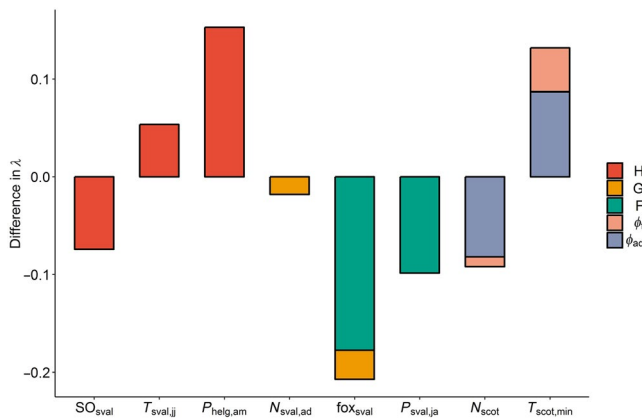| Covariate	Covariate description	Vital rate	λ_{5th}	λ_{95th}
SO_{sval}	Julian day of spring onset, Svalbard	H	1.09 (1.01, 1.18)	1.01 (0.96, 1.08)
$T_{sval,jj}$	(Mid) June–July temperature, Svalbard	H	1.02 (0.96, 1.09)	1.07 (1.00, 1.15)
$P_{helg,am}$	April–May precipitation, Helgeland	H	0.98 (0.93, 1.04)	1.12 (1.03, 1.20)
fox_{sval}	Fox abundance proxy, Svalbard	G, F	1.15 (1.08, 1.21)	0.93 (0.90, 0.97)
$N_{sval,ad}$	Local adult population size, Svalbard	G	1.06 (0.99, 1.13)	1.04 (0.98, 1.10)
$P_{sval,ja}$	(Mid) July–August precipitation, Svalbard	F	1.09 (1.02, 1.16)	0.98 (0.93, 1.04)
N_{scot}	Flyway population size, Scotland	ϕ_f, ϕ_{ad}	1.10 (1.03, 1.17)	1.01 (0.94, 1.07)
$T_{scot,min}$	Min. winter temperature, Scotland	ϕ_f, ϕ_{ad}	0.97 (0.92, 1.03)	1.10 (1.03, 1.18)

FIGURE 6 The difference in population growth rate λ when covariates on the x-axis were calculated at the 95th versus 5th quantile of their observed range. Colours represent the relative contribution of associated vital rates (H, G, F, ϕ_f and ϕ_{ad}) to these differences in the population growth rate

The population growth rate was reduced when vital rates were estimated at an early (95th quantile) and late (5th quantile) date of spring onset in Svalbard (SO_{sval}), which was attributed to reduced hatching success (H) rather than egg laying which could not be included in the analysis of the population projection matrix (Table 1; Figure 6). $T_{sval,jj}$ had a similarly large effect on λ, while carryover effects of $P_{helg,am}$ had a larger positive effect via hatching success (Table 1). Increased Arctic fox abundance (fox_{sval}) reduced λ from positive to negative growth, mostly through effects on fledging probability (F), but also on G (Figure 6). Minimum winter temperature in Scotland ($T_{scot,min}$) had a strong positive effect on survival rates and, thereby, a large contribution to variation in λ, predominantly through adult survival (Figure 6).

4 | DISCUSSION

Here, we have demonstrated how rapid climate change in high-arctic Svalbard increased barnacle goose egg production and hatching success, through positive effects of advanced spring onset and warmer summers, respectively (Figures 2, 3, and 5). However, these positive effects of climate change on early reproduction were offset by a temporal decline in fledging probability due to increased predator abundance, strongly affecting population growth (Figures 5 and 6). Although there was a positive effect of winter temperatures at Solway Firth on adult survival (Figure 4) and a positive carryover effect of rainfall at the spring stopover site on egg production (Figure 3), these drivers outside the breeding season exhibited no trend during the study. In contrast, a steady increase in total flyway population size caused negative trends in overwinter survival and carryover effects on egg production. As a likely net result of these opposing trends in population-dynamic drivers, across the annual cycle, there was no trend in local population size (Figure 5).

4.1 | Breeding season

Due to the short Arctic summer and constrained plant growing period, the time window for reproduction is highly constrained in Arctic herbivores. Timing of breeding is therefore one of the main determinants of reproductive success in Arctic nesting geese (Cooke, Rockwell, & Lank, 1995; Skinner, Jefferies, Carleton, Abraham, & Dagger, 1998). Capital breeding is a common strategy in high latitude environments (Gustine, Barboza, & Lawler, 2010; Kerby & Post, 2013), allowing feeding and reproduction to be partially decoupled in space and time (Jönsson, 1997; Newton, 1977; Sainmont, Andersen, Varpe, & Visser, 2014). For Arctic geese, this allows them to allocate nutrients from the wintering grounds and spring stopover sites to reproduction (Drent & Daan, 1980; Hahn et al., 2011).

In this study, clutch success and clutch size were negatively affected by the date of spring snow melt. The timing of snow melt largely dictates when individuals can start breeding and is an important determinant of breeding success in Arctic geese (i.e. greater snow geese, *Chen caerulescens*, Reed, Gauthier, & Giroux, 2004; pink-footed geese, *Anser brachyrhynchus*, Madsen et al., 2007; pale-bellied brent geese, *Branta bernicla hrota*, Barry, 1962). Later spring onset also reduced clutch sizes, likely since individuals that delay nesting use retained reserves for their own maintenance instead of for egg production (Davies & Cooke, 1983; Ryder, 1970).

Long-distance migrants occupy several spatially distinct locations with contrasting habitats, and individuals can therefore be affected by multiple climate and density regimes across their annual cycle (Norris & Taylor, 2005). Consequently, the combination of reproductive and migratory strategies can result in a large contribution of carryover effects to population dynamics (Inger et al., 2010; Morrissette et al., 2010). In our study population, spring precipitation had a positive effect, and overwintering population size had a negative effect, on clutch size. Although food resources at the spring stopover site on mainland Norway are generally abundant due to a predominance of agricultural land, a rainier spring is possibly associated with improved food quality since it slows down the plant growing season, resulting in higher leaf protein content (Bø & Hjeljord, 1991; Doiron, Gauthier, & Lévesque, 2014; Jonasson, Bryant, Chapin III, & Andersson, 1986). This, in turn, improves body condition and energy stores in herbivores (Mysterud, Langvatn, Yoccoz, & Chr, 2001; Ydenberg & Prins, 1981).

In many northern herbivores, spring plant phenology controls the timing of reproduction and therefore reproductive success (Langvatn, Albon, Burkey, & Clutton-Brock, 1996; Post, Bøving, Pedersen, & MacArthur, 2003; Sedinger & Raveling, 1986). Warmer summer temperatures were negatively correlated with the date of plant growth onset and increased hatching success in this barnacle goose population. Similar effects of the timing of plant growth onset have been found in other goose populations (Cooke et al., 1995; Prop & de Vries, 1993). Warmer temperatures advance the timing of plant availability and can enhance plant productivity (Jia et al., 2009) which, at such high latitudes, does not necessarily mean a strong reduction in forage quality. For nesting geese, this can reduce their foraging time away from the nest, increasing hatching success (Black et al., 2014; Greve, Elvebakk, & Gabrielsen, 1998; Prop & de Vries, 1993). In support of our findings, several breeding populations of waterfowl (including barnacle geese) in Zackenberg, eastern Greenland, suffered almost complete breeding failure because of extremely late snow melt and onset of plant growth in 2018 (Jannik Hansen, personal communication).

In highly seasonal environments such as the high Arctic, the dynamics of herbivore populations are strongly linked to seasonality in resource availability since their body condition, and thus reproductive success, is dependent on when vegetation is available (Albon et al., 2017; Douhard et al., 2013; Langvatn et al., 1996; Sæther, 1997). Many species of herbivores, and especially waterfowl such as geese, are precocial, that is, offspring leave the nest early and in a relatively developed state. Goslings are largely dependent on their own resource acquisition and are vulnerable to fluctuations in food (vegetation) resources (Lindholm, Gauthier, & Desrochers, 1994; Loonen, Bruinzeel, Black, & Drent, 1999). Plant productivity has been identified as a key driver of gosling growth rates in several species and limited food supply increases pre-fledging mortality (Lindholm et al., 1994; Loonen, Oosterbeek, & Drent, 1997; Williams, Cooch, Jefferies, & Cooke, 1993). Increased precipitation during the peak plant growing season had a negative effect on fledging success in this study population. The mechanisms behind this remain uncertain but could be related to cloud clover and generally poorer plant growing conditions, reducing the standing crop of an important food source, the grass *P. arctica*.

However, these effects of weather in early reproductive phases were largely offset by predation of goslings. Predation by Arctic foxes is the main top-down regulator of reproduction in many Arctic nesting goose populations, causing annual fluctuations in egg productivity and gosling survival (Bêty et al., 2002; Gauthier et al., 2004; Loonen et al., 1998; Samelius & Alisauskas, 2000). In our study population, the brood-rearing phase is when offspring are most vulnerable to predation (Loonen et al., 1998) and increased local abundance of Arctic foxes over time had a dramatic negative effect on gosling survival (i.e. fledging success).

Previous studies of Arctic geese have indicated density-dependent effects during the breeding season (Cooch, Lank, Rockwell, & Cooke, 1989; Larsson & Forslund, 1994; Layton-Matthews et al., 2019), through competition for food (e.g. Larsson & Forslund, 1994; Loonen et al., 1997) and nesting sites (Ebbinge et al., 2002). This study lends some support for food competition as the main driver, since the number of goslings per parent (i.e. family size) had a negative effect on the proportion fledging. Barnacle geese provide parental care through vigilance and warming, and this parental care decreases with increasing family size (Forslund, 1993), which would then appear as 'negative density dependence'.

4.2 | Non-breeding season

Both weather and density-dependent effects at the wintering grounds caused annual variation in survival. Winter conditions influence body condition in Arctic herbivores via effects on resource availability (Albon et al., 2017; Guillemain, Elmberg, Arzel, Johnson, & Simon, 2008; Miller & Barry, 2009). Effects of varying overwinter resources are less well documented for migratory herbivores but could be important in terms of direct mortality as well as carryover effects later in the annual cycle. In Arctic geese, body reserves are fundamental for surviving migration (Klaassen et al., 2014; Owen & Black, 1989, 1991b; Prop & Black, 1998). Higher average daily minimum temperature in Scotland during winter increased survival rates of both fledglings and adults, increasing population growth. Poor weather conditions at the wintering grounds have been shown to reduce overwintering survival in other goose species (Kery, Madsen, & Lebreton, 2006; Owen & Black, 1991b; Schaub, Kania, & Köppen, 2005). Severe winters, with extended periods below freezing, reduce plant availability and productivity through

frost damage and increased snow cover (Fox, Elmberg, Tombre, & Hessel, 2017). Barnacle geese are probably most food limited in mid-winter, resulting in reduced body condition until initiation of plant productivity in February–March, prior to the spring migration from Scotland (Owen, Wells, & Black, 1992). A large proportion of natural mortality also likely occurs during autumn migration (Owen, 1982; Owen & Black, 1991a). However, in an East-Atlantic population of pale-bellied brent geese, survival was also extremely low in severe winters with food depletion (Clausen, Frederiksen, Percival, Anderson, & Denny, 2001) and in the Pacific black brant, *Branta bernicla*, mortality largely occurred during late spring due to disease, predation and starvation (Ward, Rexstad, Sedinger, Lindberg, & Dawe, 1997). Thus, although the mechanisms and timing vary, environmental conditions during the non-breeding season seem an important source of natural mortality and carryover effects on reproduction.

Despite the dramatic increases in Arctic goose populations globally, there has been little evidence of density regulation through flyway populations at the wintering grounds (Kery et al., 2006; Larsson & Forslund, 1994; Trinder, 2014). This is likely explained by continued range expansion in the Arctic, as well as temperate wintering grounds (Fox et al., 2010), and improved food quality due to the transition to agricultural land (Fox & Abraham, 2017), which have facilitated this continued growth. However, we observed a negative effect of the total flyway population on annual survival rates and a carryover effect on clutch size. Consequently, density dependence may have begun to play an increasing role in regulating goose population growth, although its effects are only apparent in local, well-established populations but not at the flyway population level (Layton-Matthews et al., 2019; Trinder, 2014). Survival estimates from populations at the wintering grounds are inflated by individuals from newly colonized areas in the Arctic, where resources are temporarily in excess. Thus, despite the increase in carrying capacity (Van Eerden, 1996), density-dependent processes at the wintering grounds may have important implications for future management of Arctic goose populations. Flyway population size affected survival more in adults than fledglings, whose autumn migration is a more likely cause of mortality (Owen & Black, 1989). However, the strength of the density dependence found here should be interpreted with caution, as removal of the trend from N_{scot} (i.e. accounting for increases in carrying capacity) reduced its effect on survival rates (to −0.04; −0.11, −0.01).

4.3 | Net implications of climate change

The dramatic warming of the Arctic (Stocker et al., 2014) has resulted in an earlier snow-free tundra, advanced plant phenology and increased productivity. We show that this has benefitted barnacle geese in the early reproductive stages by increasing clutch success, clutch size and hatching success over time. However, the potential benefits of advanced phenology likely depend on the capacity of Arctic geese to align their migratory cues (Lameris et al., 2017), thereby avoiding trophic mismatch. In some Arctic species, migratory strategies are relatively dynamic (Clausen, Madsen, Cottaar, Kuijken, & Verscheure, 2018; Eichhorn, Drent, Stahl, Leito, & Alerstam, 2009; Lameris et al., 2017); however, migration timing is at least partially fixed (Kölzsch et al., 2015; Lameris et al., 2018; Van der Jeugd et al., 2009). The reliability of resources at spring stopover sites will also determine their ability to respond to future change (Fox et al., 2014; Prop, Black, & Shimmings, 2003). Furthermore, although the timing of spring onset and vegetation green-up contributed substantially to variation in population growth (i.e. the retrospective analysis), so did a change in predation pressure from Arctic foxes. Consequently, the potential benefits of an advancing and warming Arctic for early reproductive stages are offset by indirect climate change effects limiting later reproductive stages. The tendency for increasing fox numbers, which is likely the main explanation for the observed strong decline in fledging probability, seems mainly a result of the irruptive population of reindeer (*Rangifer tarandus platyrhynchus*) in this area, following their reintroduction (Aanes, Sæther, & Øritsland, 2000; Fuglei et al., 2003). Reindeer carcasses represent an important food source for Arctic foxes in winter and spring. High carcass availability in spring (e.g. following harsh winters) also boosts fox pup production (Hansen et al., 2013). Since the abundance of Svalbard reindeer is generally increasing because of climate warming (e.g. Albon et al., 2017), an overall higher fox density may be likely in the future. This would restrict growth in goose populations directly though the predation of eggs and juveniles (McDonald, Roth, & Baldwin, 2017) and potentially indirectly by increasing density-dependent effects through a reduction in the available foraging area for geese (Loonen et al., 1998). A steady increase in breeding populations of geese in general is likely having a further positive effect on fox pup overwinter survival (Ims et al., 2013). Additionally, recently increasing numbers of polar bears, *Ursus maritimus*, 'stranded' by the loss of sea ice, have resulted in severe declines in hatching success in some breeding populations of geese on Svalbard (Prop et al., 2015). Thus, increased predation pressure by Arctic foxes and polar bears—that is, indirect climate change effects—may counteract the benefits of climate warming for early stages of reproduction, contributing to the lack of a positive trend in local population size.

No temporal trend was observed in winter climate in Scotland. Nevertheless, moderately warmer and wetter winters are predicted for Scotland under future global warming, with fewer frost days and an earlier growing season (Jacob et al., 2014; Jenkins, Perry, & Prior, 2009). According to our results, this would reduce goose mortality with a large effect on local population growth. However, the consequences of warmer winters for plant productivity, and therefore barnacle geese, are still uncertain (Crawford, 1997; Kreyling, 2010).

In conclusion, current and near-future climate change involves contrasting trends in important environmental drivers across migratory stages and therefore does not necessarily pose a negative outlook for Arctic geese. Earlier springs and warmer summers appear beneficial for reproduction in populations where individuals can sufficiently adjust their phenology (but see Lameris et al., 2018), and even a slight future warming trend at the wintering grounds may increase survival. However, extrapolation

to future levels of warming is problematic (Bilt et al., 2019) and changes occurring further up the food web may counteract bottom-up benefits of Arctic warming. Additionally, and importantly, our results indicate that density regulation both at the breeding grounds in Svalbard and, especially, at the wintering grounds in the United Kingdom, will act to curb population growth caused by climate change.

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SUPPORTING INFORMATION

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