

University of Groningen

Contrasting consequences of climate change for migratory geese

Layton-Matthews, Kate; Hansen, Brage Bremset; Grotan, Vidar; Fuglei, Eva; Loonen, Maarten J. J. E.

Published in:
Global Change Biology

DOI:
[10.1111/gcb.14773](https://doi.org/10.1111/gcb.14773)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2020

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Layton-Matthews, K., Hansen, B. B., Grotan, V., Fuglei, E., & Loonen, M. J. J. E. (2020). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology*, *26*(2), 642-657.
<https://doi.org/10.1111/gcb.14773>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

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

Kate Layton-Matthews¹  | Brage Bremset Hansen¹  | Vidar Grøtan¹ | Eva Fuglei² | Maarten J. J. E. Loonen³

¹Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

²Norwegian Polar Institute, Tromsø, Norway

³Arctic Centre, University of Groningen, Groningen, The Netherlands

Correspondence

Kate Layton-Matthews, Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway.
Email: kate.l.matthews@ntnu.no

Funding information

Research Council of Norway, Grant/Award Number: 276080, 244647, 273451 and 223257; Nederlandse Organisatie voor Wetenschappelijk Onderzoek; EU; Organization for Scientific Research NWO; Ministry of Foreign Affairs; BIRDHEALTH, Grant/Award Number: 851.40.071; Geese on Arctic Tundra, Grant/Award Number: 866.12.407; Norwegian Polar Institute; University of Groningen

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.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd

KEYWORDS

Arctic amplification, Arctic geese, barnacle goose, carryover effects, climate change, migration, population dynamics, trophic interactions

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 (Béty, 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.

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

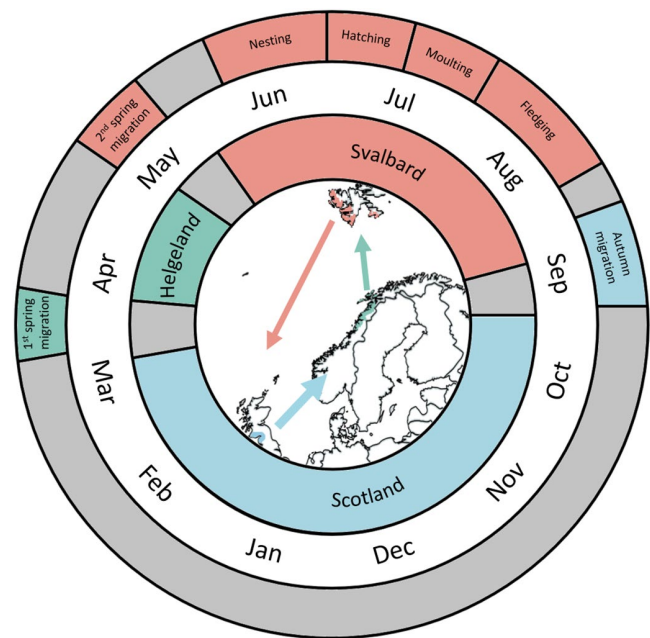


FIGURE 1 Migration route and timing of key events for Svalbard barnacle geese. Barnacle geese overwinter at Solway Firth, Scotland (blue), before travelling to western Svalbard for breeding (pink) via a stopover on the coast of mainland Norway (green). The timing of migrations and reproductive events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

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 ($T_{\text{scot,min}}$, $T_{\text{scot,max}}$, 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 ($T_{\text{helg,am}}$, $P_{\text{helg,am}}$). 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 ($\text{snow}_{\text{sval}}$; 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 ($T_{\text{sval,jj}}$, $P_{\text{sval,jj}}$) and mid-July to mid-August ($T_{\text{sval,ja}}$, $P_{\text{sval,ja}}$). 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 ($N_{\text{sval,ad}}$), 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 $T_{\text{sval,jj}}$ 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. $P_{\text{sval,ja}}$ 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 step-wise 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 $T_{helg,sum6}$ at Helgeland (i.e. carryover effects) and SO_{sval} , snw_{sval} and $N_{sval,ad}$ on Svalbard. The candidate model set of hatching (H and G) included $T_{sval,ji}$, $P_{sval,ji}$, 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

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

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} .

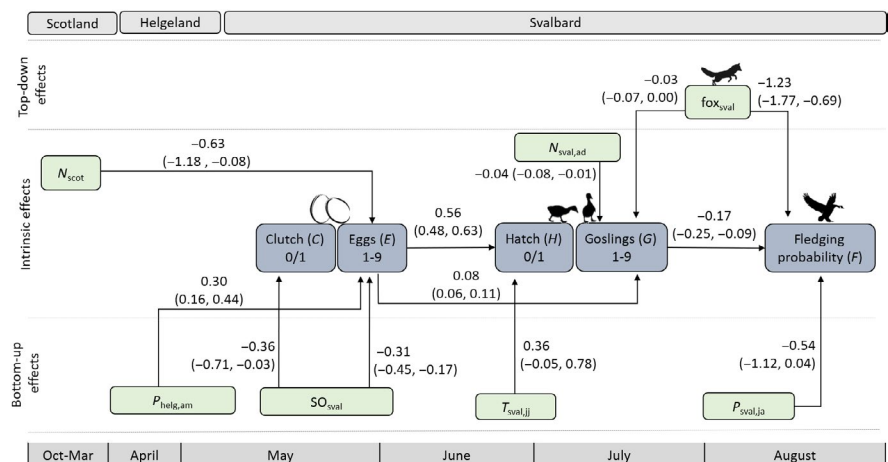


FIGURE 2 Best-fitting path model diagram for the reproductive stages, with standardized slope coefficients and associated 95% confidence intervals in brackets

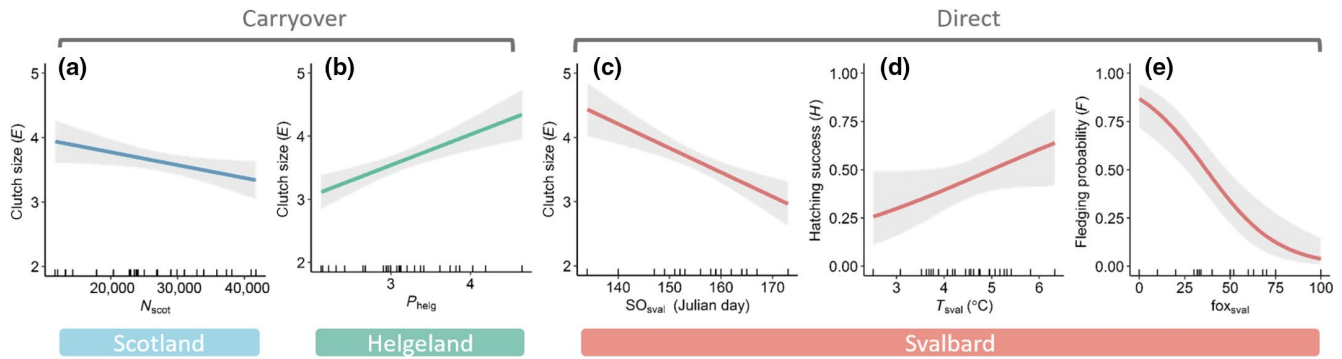


FIGURE 3 Model predictions with 95% confidence intervals, describing (a, b) the carryover effects of (a) flyway population size in Scotland (N_{scot}) and (b) spring precipitation at Helgeland ($P_{helg,am}$), and (c–e) the direct effects of (c) the onset of spring (SO_{sval}) at the Svalbard breeding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

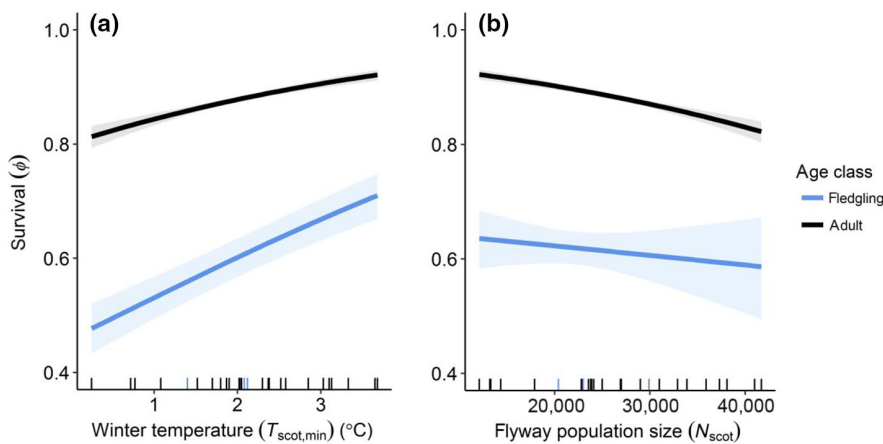


FIGURE 4 Model predictions with 95% confidence intervals describing the effect of (a) Scotland winter temperature ($T_{scot,min}$) and (b) total flyway population size (N_{scot}) on the survival rate of fledglings (ϕ_f) and adults (ϕ_{ad}). Data distributions are shown on the x-axis as rugs

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 ($P_{N_{sval,ad}} = 0.07$; $P_{fox_{sval}} = 0.08$). A weak positive effect of $T_{sval,ij}$ and a weak negative effect of $P_{sval,ij}$ 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 $P_{sval,ja}$ ($\Delta AIC_c = 1.29$) 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 ($T_{sval,ij}$) and the date of plant growth onset (-0.78 ;

$-1.15, -0.41$; $R^2 = 0.61$). $T_{sval,ij}$ 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 ($P_{helg,apr,my}$) 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 ($\Delta AIC_c = 4.18$) 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 ($T_{\text{sval,ij}}$) 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, $P_{\text{sval,ja}}$ (0.00 ; -0.05 , 0.05), mean minimum temperature in Scotland, $T_{\text{scot,min}}$ (0.00 ; -0.04 , 0.05 ; Appendix S6), and adult population size in Svalbard, $N_{\text{sval,ad}}$ (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).

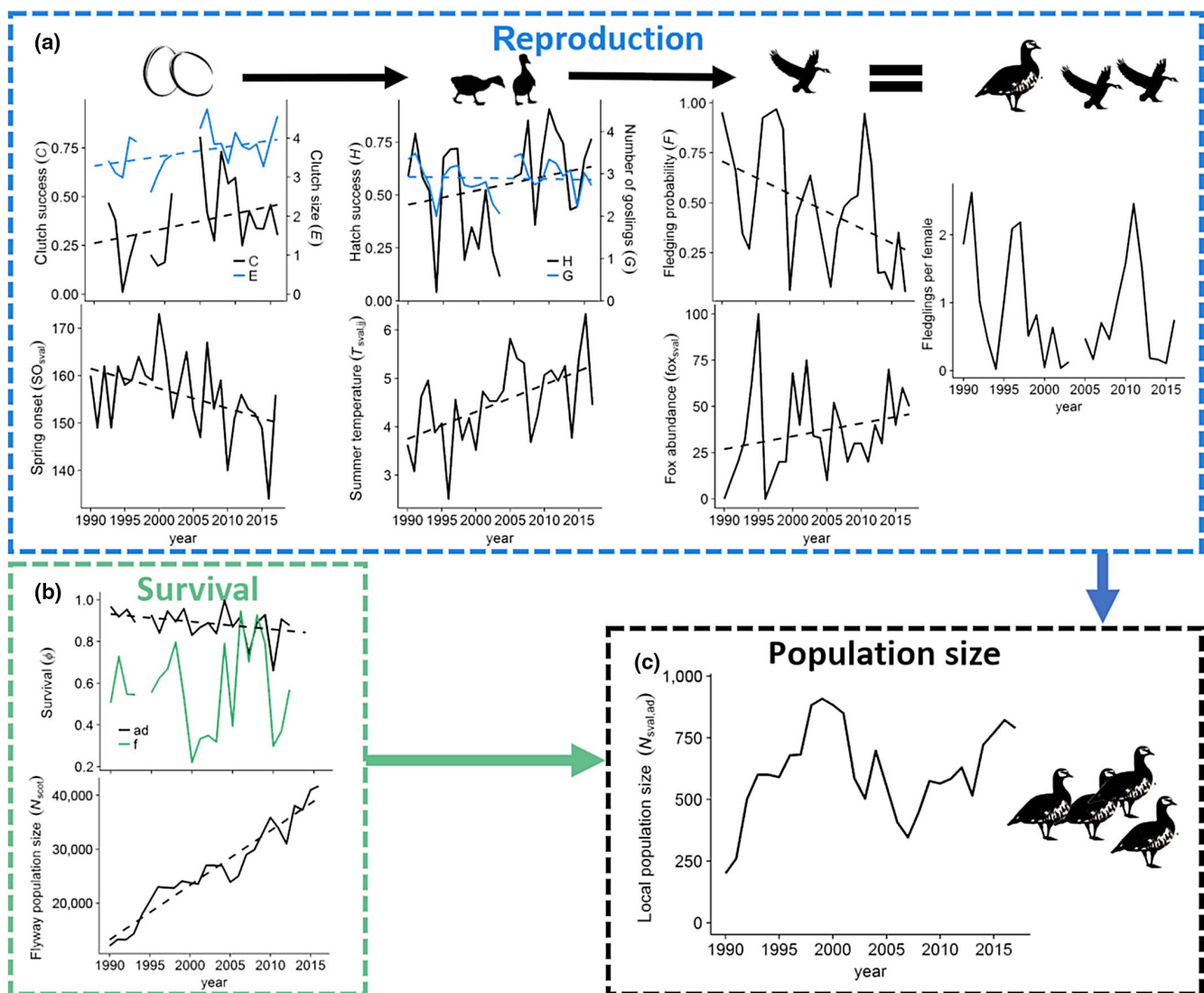


FIGURE 5 Trends in barnacle geese parameters and associated explanatory variables. For reproduction, from left to right: (a) clutch success (C) and clutch size (E) and the predictor spring onset (SO_{sval}); hatch success (H) and the predictor mid-June to mid-July temperature ($T_{\text{sval,ij}}$); 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 ($N_{\text{sval,ad}}$)

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)

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

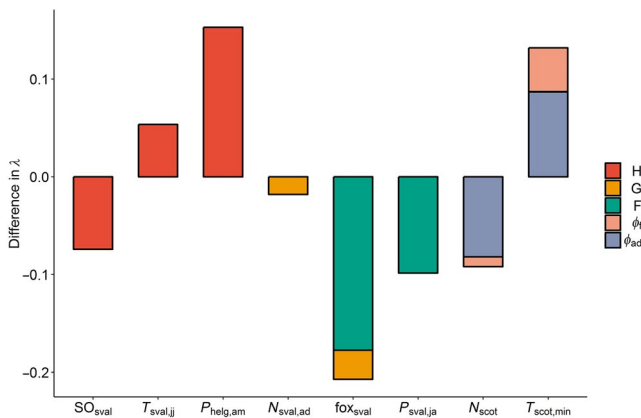


FIGURE 6 The difference in population growth rate λ when covariates on the x-axis were calculated at the 95th versus 5th quantile of their observed range. Colours represent the relative contribution of associated vital rates (H , G , F , ϕ_f and ϕ_{ad}) to these differences in the population growth rate

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 cover 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, Elmer, 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, & Verschuere, 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 through 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.

ACKNOWLEDGEMENTS

We thank the large team of scientists, students and volunteers from the University of Groningen, who helped collecting and processing the data. Permissions by the Governor of Svalbard, the Bird Ringing Centre, Stavanger, the Animal Experimentation Board of Norway (FOTS) and the UK Wildfowl and Wetlands Trust made the fieldwork possible. We thank Stein Rune-Karlsen at Norut, Tromsø for kindly providing the onset of plant growth time series for Ny-Ålesund (Appendix S2) and Mari Aas Fjellidal for advice on the manuscript. The Netherlands Arctic and Polar Program, managed by the Netherlands Organization for Scientific Research NWO, and the Ministry of Foreign Affairs via support to the Netherlands Arctic Station, and the projects BIRDHEALTH (851.40.071) and Geese on Arctic Tundra (866.12.407) provided funding for data collection in Ny-Ålesund. The Norwegian Polar Institute provided funding for the annual den site monitoring of arctic fox. The European Union supported FP7-project FRAGILE and the University of Groningen gave additional support. This work was supported by the Research Council of Norway (FRIMEDBIO grant number 276080, KLIMAFORSK 244647 and 273451 and Centre of Excellence 223257).

ORCID

Kate Layton-Matthews  <https://orcid.org/0000-0001-5275-1218>

Brage Bremset Hansen  <https://orcid.org/0000-0001-8763-4361>

REFERENCES

- Aanes, R., Sæther, B. E., & Øritsland, N. A. (2000). Fluctuations of an introduced population of Svalbard reindeer: The effects of density dependence and climatic variation. *Ecography*, 23(4), 437–443. <https://doi.org/10.1034/j.1600-0587.2000.230406.x>
- Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., ... Duff, E. I. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, 23(4), 1374–1389. <https://doi.org/10.1111/gcb.13435>
- Angerbjorn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator-prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, 68(1), 34–49. <https://doi.org/10.1046/j.1365-2656.1999.00258.x>
- Arft, A., Walker, M., Gurevitch, J., Alatalo, J., Bret-Harte, M., Dale, M., ... Wookey, P.A. (1999). Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, 69(4), 491–511. <https://doi.org/10.2307/2657227>
- Barrio, I. C., Bueno, C. G., Gartzia, M., Soininen, E. M., Christie, K. S., Speed, J. D., ... Horstkotte, T. (2016). Biotic interactions mediate patterns of herbivore diversity in the Arctic. *Global Ecology and Biogeography*, 25(9), 1108–1118. <https://doi.org/10.1111/geb.12470>
- Barry, T. W. (1962). Effect of late seasons on Atlantic Brant reproduction. *The Journal of Wildlife Management*, 26(1), 19–26. <https://doi.org/10.2307/3798163>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. R package version 1.1-10. *Journal of Statistical Software*, 67(1), 1–48.
- Bazely, D., & Jefferies, R. (1989). Leaf and shoot demography of an arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. *Journal of Ecology*, 77, 811–822. <https://doi.org/10.2307/2260987>
- Bêty, J., Gauthier, G., & Giroux, J.-F. (2003). Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. *The American Naturalist*, 162(1), 110–121. <https://doi.org/10.1086/375680>
- Bêty, J., Gauthier, G., Korpimäki, E., & Giroux, J. (2002). Shared predators and indirect trophic interactions: Lemming cycles and arctic-nesting geese. *Journal of Animal Ecology*, 71(1), 88–98. <https://doi.org/10.1046/j.0021-8790.2001.00581.x>
- Bilt, W., Bakke, J., Smedsrud, L., Sund, M., Schuler, T., Westermann, S., ... Sorteberg, A. (2019). Climate in Svalbard 2100 – A knowledge base for climate adaptation. Technical report from Norwegian Centre for Climate Services Reports (1/2019).
- Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M., & Henry, G. H. (2015). Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, 21(12), 4651–4661. <https://doi.org/10.1111/gcb.13051>
- Black, J. M., Prop, J., & Larsson, K. (2014). Survival and reproduction. In J. Martin (Ed.), *The barnacle goose* (pp. 159–172). London, UK: Bloomsbury Publishing.
- Bø, S., & Hjeljord, O. (1991). Do continental moose ranges improve during cloudy summers? *Canadian Journal of Zoology*, 69(7), 1875–1879. <https://doi.org/10.1139/z91-260>
- Both, C., Bouwhuis, S., Lessells, C., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81–83. <https://doi.org/10.1038/nature04539>
- Bruggeman, J. E., Swem, T., Andersen, D. E., Kennedy, P. L., & Nigro, D. (2015). Dynamics of a recovering Arctic bird population: The importance of climate, density dependence, and site quality. *Ecological Applications*, 25(7), 1932–1943. <https://doi.org/10.1890/14-1591.1>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Caswell, H. (1989). Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling*, 46(3–4), 221–237. [https://doi.org/10.1016/0304-3800\(89\)90019-7](https://doi.org/10.1016/0304-3800(89)90019-7)
- Caswell, H. (2001). *Matrix population models*. Sunderland, MA: Sinauer Associates Inc.
- Clausen, K. K., & Clausen, P. (2013). Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia*, 173(3), 1101–1112. <https://doi.org/10.1007/s00442-013-2681-0>
- Clausen, K. K., Madsen, J., Cottaar, F., Kuijken, E., & Verschuere, C. (2018). Highly dynamic wintering strategies in migratory geese: Coping with environmental change. *Global Change Biology*, 24(7), 3214–3225. <https://doi.org/10.1111/gcb.14061>
- Clausen, P., Frederiksen, M., Percival, S., Anderson, G., & Denny, M. (2001). Seasonal and annual survival of East-Atlantic Pale-bellied Brent Geese *Branta hrota* assessed by capture-recapture analysis. *Ardea*, 89(special issue), 101–112.
- Cooch, E., Lank, D., Rockwell, R., & Cooke, F. (1989). Long-term decline in fecundity in a Snow Goose population: Evidence for

- density dependence? *Journal of Animal Ecology*, 711–726. <https://doi.org/10.2307/4858>
- Cooke, F., Rockwell, R. F., & Lank, D. B. (1995). The timing of reproduction. In C. M. Perrins (Ed.), *The snow geese of La Pérouse Bay* (pp. 189–212). Oxford, UK: Oxford University Press.
- Crawford, R. (1997). Oceanicity and the ecological disadvantages of warm winters. *Botanical Journal of Scotland*, 49(2), 205–221. <https://doi.org/10.1080/03746609708684867>
- Davies, J. C., & Cooke, F. (1983). Annual nesting productivity in snow geese: Prairie droughts and arctic springs. *The Journal of Wildlife Management*, 47(2), 291–296. <https://doi.org/10.2307/3808501>
- Dickey, M. H., Gauthier, G., & Cadieux, M. C. (2008). Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology*, 14(9), 1973–1985. <https://doi.org/10.1111/j.1365-2486.2008.01622.x>
- Doiron, M., Gauthier, G., & Lévesque, E. (2014). Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *Journal of Ecology*, 102(2), 508–517. <https://doi.org/10.1111/1365-2745.12213>
- Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, 21(12), 4364–4376. <https://doi.org/10.1111/gcb.13057>
- Douhard, M., Gaillard, J.-M., Delorme, D., Capron, G., Duncan, P., Klein, F., & Bonenfant, C. (2013). Variation in adult body mass of roe deer: Early environmental conditions influence early and late body growth of females. *Ecology*, 94(8), 1805–1814. <https://doi.org/10.1890/13-0034.1>
- Drent, R., & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea*, 55(1–2), 225–252. <https://doi.org/10.5253/arde.v68.p225>
- Ebbinge, B. S., Heesterbeek, J., Ens, B. J., & Goedhart, P. W. (2002). Density dependent population limitation in dark-bellied brent geese *Branta b. bernicla*. *Avian Science*, 2(2), 63–75.
- Ehrich, D., Cerezo, M., Rodnikova, A. Y., Sokolova, N. A., Fuglei, E., Shtro, V. G., & Sokolov, A. A. (2017). Vole abundance and reindeer carcasses determine breeding activity of Arctic foxes in low Arctic Yamal, Russia. *BMC Ecology*, 17(1), 32. <https://doi.org/10.1186/s12898-017-0142-z>
- Eichhorn, G., Drent, R. H., Stahl, J., Leito, A., & Alerstam, T. (2009). Skipping the Baltic: The emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology*, 78(1), 63–72. <https://doi.org/10.1111/j.1365-2656.2008.01485.x>
- Eide, N. E., Stien, A., Prestrud, P., Yoccoz, N. G., & Fuglei, E. (2012). Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. *Journal of Animal Ecology*, 81(3), 640–648. <https://doi.org/10.1111/j.1365-2656.2011.01936.x>
- Fauchald, P., Park, T., Tømmervik, H., Myneni, R., & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science Advances*, 3(4), e1601365. <https://doi.org/10.1126/sciadv.1601365>
- Forchhammer, M. C., Post, E., Stenseth, N. C., & Boertmann, D. M. (2002). Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology*, 44(2), 113–120. <https://doi.org/10.1007/s101440200013>
- Forchhammer, M. C., Schmidt, N. M., Høye, T. T., Berg, T. B., Hendrichsen, D. K., & Post, E. (2008). Population dynamical responses to climate change. *Advances in Ecological Research*, 40, 391–419. [https://doi.org/10.1016/S0065-2504\(07\)00017-7](https://doi.org/10.1016/S0065-2504(07)00017-7)
- Forslund, P. (1993). Vigilance in relation to brood size and predator abundance in the barnacle goose, *Branta leucopsis*. *Animal Behaviour*, 45(5), 965–973. <https://doi.org/10.1006/anbe.1993.1115>
- Forslund, P., & Larsson, K. (1992). Age-related reproductive success in the barnacle goose. *Journal of Animal Ecology*, 61, 195–204. <https://doi.org/10.2307/5522>
- Foster, J. (1989). The significance of the date of snow disappearance on the Arctic tundra as a possible indicator of climate change. *Arctic and Alpine Research*, 21(1), 60–70. <https://doi.org/10.2307/1551517>
- Fox, A. D., & Abraham, K. F. (2017). Why geese benefit from the transition from natural vegetation to agriculture. *Ambio*, 46(2), 188–197. <https://doi.org/10.1007/s13280-016-0879-1>
- Fox, A. D., Ebbinge, B. S., Mitchell, C., Heinicke, T., Aarvak, T., Colhoun, K., ... Koffijberg, K. (2010). Current estimates of goose population sizes in western Europe, a gap analysis and assessment of trends. *Ornis Svecica*, 20, 115–127. <https://doi.org/10.34080/os.v20.19922>
- Fox, A. D., Elmberg, J., Tombre, I. M., & Hessel, R. (2017). Agriculture and herbivorous waterfowl: A review of the scientific basis for improved management. *Biological Reviews*, 92(2), 854–877. <https://doi.org/10.1111/brv.12258>
- Fox, A. D., & Madsen, J. (2017). Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio*, 46(2), 179–187. <https://doi.org/10.1007/s13280-016-0878-2>
- Fox, A. D., Weegman, M. D., Bearhop, S., Hilton, G. M., Griffin, L., Stroud, D. A., & Walsh, A. (2014). Climate change and contrasting plasticity in timing of a two-step migration episode of an Arctic-nesting avian herbivore. *Current Zoology*, 60(2), 233–242. <https://doi.org/10.1093/czoolo/60.2.233>
- Frederiksen, M., & Bregnballe, T. (2000). Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. *Journal of Animal Ecology*, 69(5), 737–752. <https://doi.org/10.1046/j.1365-2656.2000.00435.x>
- Fuglei, E., Øritsland, N. A., & Prestrud, P. (2003). Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology*, 26(2), 93–98. <https://doi.org/10.1007/s00300-002-0458-8>
- Fujita, M., & Kameda, K. O. (2016). Nutrient dynamics and nutrient cycling by birds. In Ç. H. Sekercioglu, D. G. Wenny, & C. J. Whelan (Eds.), *Why birds matter: Avian ecological function: Nutrient dynamics and nutrient cycling by birds* (pp. 271–291). Chicago, IL: The University of Chicago Press.
- Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, 84(12), 3294–3306. <https://doi.org/10.1890/02-0409>
- Gareth, K. (2004). Predicting impacts of Arctic climate change: Past lessons and future challenges. *Ecological Research*, 19(1), 65–74. <https://doi.org/10.1111/j.1440-1703.2003.00609.x>
- Gauthier, G., Bêty, J., Giroux, J.-F., & Rochefort, L. (2004). Trophic interactions in a high arctic snow goose colony. *Integrative Comparative Biology*, 44(2), 119–129. <https://doi.org/10.1093/icb/44.2.119>
- Gelman, A., & Hill, J. (2006). Causal inference using multilevel models. In *Data analysis using regression and multilevel/hierarchical models* (pp. 503–512). Cambridge, UK: Cambridge University Press.
- Greve, I. A., Elvebakk, A., & Gabrielsen, G. W. (1998). Vegetation exploitation by barnacle geese *Branta leucopsis* during incubation on Svalbard. *Polar Research*, 17(1), 1–14. <https://doi.org/10.3402/polar.v17i1.6603>
- Guillemain, M., Elmberg, J., Arzel, C., Johnson, A. R., & Simon, G. (2008). The income–capital breeding dichotomy revisited: Late winter body condition is related to breeding success in an income breeder. *Ibis*, 150(1), 172–176. <https://doi.org/10.1111/j.1474-919x.2007.00700.x>
- Gustine, D. D., Barboza, P. S., & Lawler, J. P. (2010). Dynamics of body protein and the implications for reproduction in captive muskoxen (*Ovibos moschatus*) during winter. *Physiological Biochemical Zoology*, 83(4), 687–697. <https://doi.org/10.1086/652729>
- Hahn, S., Loonen, M. J., & Klaassen, M. (2011). The reliance on distant resources for egg formation in high Arctic breeding barnacle geese *Branta leucopsis*. *Journal of Avian Biology*, 42(2), 159–168. <https://doi.org/10.1111/j.1600-048x.2010.05189.x>
- Hansen, B. B., Gamelon, M., Albon, S. D., Lee, A. M., Stien, A., Irvine, R. J., ... Veiberg, V. (2019). More frequent extreme climate events stabilize

- reindeer population dynamics. *Nature Communications*, 10(1), 1616. <https://doi.org/10.1038/s41467-019-09332-5>
- Hansen, B. B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., ... Pedersen, Å. Ø. (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science*, 339(6117), 313–315. <https://doi.org/10.1126/science.1226766>
- Hessen, D. O., Tombre, I. M., van Geest, G., & Alfsnes, K. (2017). Global change and ecosystem connectivity: How geese link fields of central Europe to eutrophication of Arctic freshwaters. *Ambio*, 46(1), 40–47. <https://doi.org/10.1007/s13280-016-0802-9>
- Hill, G. B., & Henry, G. H. (2011). Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, 17(1), 276–287. <https://doi.org/10.1111/j.1365-2486.2010.02244.x>
- Horvitz, C., Schemske, D. W., & Caswell, H. (1997). The relative “importance” of life-history stages to population growth: Prospective and retrospective analyses. In S. Tuljapurkar & H. Caswell (Eds.), *Structured-population models in marine, terrestrial, and freshwater systems* (pp. 247–271). Boston, MA: Springer.
- Høyte, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K., & Forchhammer, M. C. (2013). Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, 3(8), 759–763. <https://doi.org/10.1038/nclimate1909>
- Hüppop, O., & Winkel, W. (2006). Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: The role of spatially different temperature changes along migration routes. *Journal of Ornithology*, 147(2), 344–353. <https://doi.org/10.1007/s10336-005-0049-x>
- Ims, R. A., Jepsen, J. U., Stien, A., & Yoccoz, N. G. (2013). *Science plan for COAT: Climate-ecological observatory for Arctic Tundra*. Tromsø, Norway: Fram Centre.
- Inger, R., Harrison, X. A., Ruxton, G. D., Newton, J., Colhoun, K., Gudmundsson, G. A., ... Bearhop, S. (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, 79(5), 974–982. <https://doi.org/10.1111/j.1365-2656.2010.01712.x>
- Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O. B., Bouwer, L. M., ... Georgievski, G. (2014). EURO-CORDEX: New high-resolution climate change projections for European impact research. *Regional Environmental Change*, 14(2), 563–578.
- Jenkins, G., Perry, M., & Prior, M. (2009). *UKCIP08: The climate of the United Kingdom and recent trends*. Exeter, UK: Met Office Hadley Centre.
- Jensen, R. A., Madsen, J., O'Connell, M., Wisz, M. S., Tømmervik, H., & Mehlum, F. (2008). Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology*, 14(1), 1–10. <https://doi.org/10.1111/j.1365-2486.2007.01461.x>
- Jia, G. J., Epstein, H. E., & Walker, D. A. (2009). Vegetation greening in the Canadian Arctic related to decadal warming. *Journal of Environmental Monitoring*, 11(12), 2231–2238. <https://doi.org/10.1039/b911677j>
- Jonasson, S., Bryant, J. P., Chapin, F. S. III, & Andersson, M. (1986). Plant phenols and nutrients in relation to variations in climate and rodent grazing. *The American Naturalist*, 128(3), 394–408. <https://doi.org/10.1086/284570>
- Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78(1), 57–66. <https://doi.org/10.2307/3545800>
- Karlsen, S. R., Anderson, H. B., Van der Wal, R., & Hansen, B. B. (2018). A new NDVI measure that overcomes data sparsity in cloud-covered regions predicts annual variation in ground-based estimates of high arctic plant productivity. *Environmental Research Letters*, 13(2), 025011. <https://doi.org/10.1088/1748-9326/aa9f75>
- Karlsen, S. R., Elvebakk, A., Høgda, K. A., & Grydeland, T. (2014). Spatial and temporal variability in the onset of the growing season on Svalbard, Arctic Norway – Measured by MODIS-NDVI satellite data. *Remote Sensing*, 6(9), 8088–8106. <https://doi.org/10.3390/rs6098088>
- Kerby, J., & Post, E. (2013). Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1624), 20120484. <https://doi.org/10.1098/rstb.2012.0484>
- Kery, M., Madsen, J., & Lebreton, J. D. (2006). Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology*, 75(5), 1172–1181. <https://doi.org/10.1111/j.1365-2656.2006.01140.x>
- Klaassen, R. H., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K. M., ... Alerstam, T. (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, 83(1), 176–184. <https://doi.org/10.1111/1365-2656.12135>
- Kohler, J., & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. *Arctic, Antarctic and Alpine Research*, 36(3), 333–341. [https://doi.org/10.1657/1523-0430\(2004\)036\[0333:eowsag\]2.0.co;2](https://doi.org/10.1657/1523-0430(2004)036[0333:eowsag]2.0.co;2)
- Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K. M., ... Nolet, B. A. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *Journal of Animal Ecology*, 84(1), 272–283. <https://doi.org/10.1111/1365-2656.12281>
- Kondratyev, A., Zaynagutdinova, E., & Kruckenberg, H. (2013). Barnacle goose *Branta leucopsis* abundance on Kolguev Island – Current status and history of population growth. *Wildfowl*, 63(63), 56–71.
- Koons, D. N., Gunnarsson, G., Schmutz, J. M., & Rotella, J. J. (2014). Drivers of waterfowl population dynamics: From teal to swans. *Wildfowl*, 4(special issue), 169–191.
- Kreyling, J. (2010). Winter climate change: A critical factor for temperate vegetation performance. *Ecology*, 91(7), 1939–1948. <https://doi.org/10.1890/09-1160.1>
- Laake, J. L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK*. Seattle, WA: Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA.
- Lameris, T. K., Scholten, I., Bauer, S., Cobben, M. M., Ens, B. J., & Nolet, B. A. (2017). Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification. *Global Change Biology*, 23(10), 4058–4067. <https://doi.org/10.1111/gcb.13684>
- Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., ... Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, 28(15), 2467–2473.e64. <https://doi.org/10.1016/j.cub.2018.05.077>
- Langvatn, R., Albon, S., Burkey, T., & Clutton-Brock, T. (1996). Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology*, 65, 653–670. <https://doi.org/10.2307/5744>
- Larsson, K., & Forslund, P. (1994). Population dynamics of the barnacle goose *Branta leucopsis* in the Baltic area: Density-dependent effects on reproduction. *Journal of Animal Ecology*, 63, 954–962. <https://doi.org/10.2307/5272>
- Layton-Matthews, K., Loonen, M. J. E., Hansen, B. B., Saether, B.-E., Coste, C. F. D., & Grøtan, V. (2019). Density-dependent population dynamics of a high Arctic capital breeder, the barnacle goose. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.13001>
- Le Moulec, M., Buchwal, A., van der Wal, R., Sandal, L., & Hansen, B. B. (2019). Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass. *Journal of Ecology*, 107(1), 436–451. <https://doi.org/10.1111/1365-2745.13036>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210x.12512>

- Lindholm, A., Gauthier, G., & Desrochers, A. (1994). Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. *Condor*, 96(4), 898–908. <https://doi.org/10.2307/1369100>
- Loonen, M. J. J. E., Bruinzeel, L. W., Black, J. M., & Drent, R. H. (1999). The benefit of large broods in barnacle geese: A study using natural and experimental manipulations. *Journal of Animal Ecology*, 68(4), 753–768. <https://doi.org/10.1046/j.1365-2656.1999.00325.x>
- Loonen, M. J. J. E., Oosterbeek, K., & Drent, R. (1997). Variation in growth of young and adult size in barnacle geese *Branta leucopsis*: Evidence for density dependence. *Ardea*, 85(2), 177–192.
- Loonen, M. J. J. E., Tombre, I. M., & Mehlum, F. (1998). Development of an arctic barnacle goose colony: Interactions between density and predation. *Norsk Polarinstitutt Skrifter*, 200, 67–80.
- Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., ... Cottaar, F. (2007). Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology*, 30(11), 1363–1372. <https://doi.org/10.1007/s00300-007-0296-9>
- Marra, P. P., Hobson, K. A., & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, 282(5395), 1884–1886. <https://doi.org/10.1126/science.282.5395.1884>
- Maturilli, M., Herber, A., & König-Langlo, G. (2015). Surface radiation climatology for Ny-Ålesund, Svalbard (78.9° N), basic observations for trend detection. *Theoretical and Applied Climatology*, 120(1), 331–339. <https://doi.org/10.1007/s00704-014-1173-4>
- McDonald, R. S., Roth, J. D., & Baldwin, F. B. (2017). Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the southern Arctic. *Polar Research*, 36(sup1), 5. <https://doi.org/10.1080/17518369.2017.1324652>
- Miller, F. L., & Barry, S. J. (2009). Long-term control of Peary caribou numbers by unpredictable, exceptionally severe snow or ice conditions in a non-equilibrium grazing system. *Arctic*, 62(2), 175–189. <https://doi.org/10.14430/arctic130>
- Morris, W. F., & Doak, D. F. (2004). Buffering of life histories against environmental stochasticity: Accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *The American Naturalist*, 163(4), 579–590. <https://doi.org/10.1086/382550>
- Morrisette, M., Bêty, J., Gauthier, G., Reed, A., & Lefebvre, J. (2010). Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird. *Oikos*, 119(7), 1181–1191. <https://doi.org/10.1111/j.1600-0706.2009.18079.x>
- Mysterud, A., Langvatn, R., Yoccoz, N. G., & Chr, N. (2001). Plant phenology, migration and geographical variation in body weight of a large herbivore: The effect of a variable topography. *Journal of Animal Ecology*, 70(5), 915–923. <https://doi.org/10.1046/j.0021-8790.2001.00559.x>
- Newton, I. (1977). Timing and success of breeding in tundra-nesting geese. In B. Stonehouse & C. Perrins (Eds.), *Evolutionary ecology* (pp. 113–126). London, UK: Macmillan Education UK.
- Newton, I. (2006). Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology*, 147(2), 146–166. <https://doi.org/10.1007/s10336-006-0058-4>
- Newton, I. (2007). Weather-related mass-mortality events in migrants. *Ibis*, 149(3), 453–467. <https://doi.org/10.1111/j.1474-919x.2007.00704.x>
- Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. *Oikos*, 109(1), 178–186. <https://doi.org/10.1111/j.0030-1299.2005.13671.x>
- Norris, D. R., & Taylor, C. M. (2005). Predicting the consequences of carry-over effects for migratory populations. *Biology Letters*, 2(1), 148–151. <https://doi.org/10.1098/rsbl.2005.0397>
- Owen, M. (1980). *Wild geese of the world: Their life history and ecology*. London, UK: BT Batsford Limited.
- Owen, M. (1982). Population dynamics of Svalbard barnacle geese 1970–1980. The rate, pattern and causes of mortality as determined by individual marking. *Aquila*, 89, 229–247.
- Owen, M., & Black, J. M. (1989). Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *The Journal of Animal Ecology*, 58(2), 603–617. <https://doi.org/10.2307/4851>
- Owen, M., & Black, J. (1991a). The importance of migration mortality in non-passerine birds. In C. Perrins, J.-D. Lebreton, & G. Horins (Eds.), *Bird population studies: Relevance to conservation and management* (pp. 360–372). New York, NY: Oxford University Press.
- Owen, M., & Black, J. M. (1991b). A note on migration mortality and its significance in goose population dynamics. *Ardea*, 79, 195–196.
- Owen, M., & Norderhaug, M. (1977). Population dynamics of Barnacle Geese *Branta leucopsis* breeding in Svalbard, 1948–1976. *Ornis Scandinavica*, 8, 161–174. <https://doi.org/10.2307/3676101>
- Owen, M., Wells, R. L., & Black, J. M. (1992). Energy budgets of wintering barnacle geese: The effects of declining food resources. *Ornis Scandinavica*, 23(4), 451–458. <https://doi.org/10.2307/3676676>
- Pedersen, Å. Ø., Stien, J., Eidesen, P. B., Ims, R. A., Jepsen, J. U., Stien, A., ... Fuglei, E. (2018). High goose abundance reduces nest predation risk in a simple rodent-free high-Arctic ecosystem. *Polar Biology*, 41, 619–627. <https://doi.org/10.1007/s00300-017-2223-z>
- Peeters, B., Pedersen, Å. Ø., Loe, L. E., Isaksen, K., Veiberg, V., Stien, A., ... Hansen, B. B. (2019). Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: Detection of a climate-cryosphere regime shift. *Environmental Research Letters*, 14(1), 015002. <https://doi.org/10.1088/1748-9326/aaefb3>
- Post, E., Bøving, P. S., Pedersen, C., & MacArthur, M. A. (2003). Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology*, 81(10), 1709–1714. <https://doi.org/10.1139/z03-172>
- Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 363(1501), 2367–2373. <https://doi.org/10.1098/rstb.2007.2207>
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., ... Høye, T. T. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325(5946), 1355–1358. <https://doi.org/10.1126/science.1173113>
- Prop, J., Aars, J., Bårdsen, B.-J., Hanssen, S. A., Bech, C., Bourgeon, S., ... Noreen, E. (2015). Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution*, 3(33). <https://doi.org/10.3389/fevo.2015.00033>
- Prop, J., & Black, J. M. (1998). Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. *Norsk Polarinstitutt Skrifter*, 200, 175–194.
- Prop, J., Black, J. M., & Shimmings, P. (2003). Travel schedules to the high arctic: Barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, 103(2), 403–414. <https://doi.org/10.1034/j.1600-0706.2003.12042.x>
- Prop, J., Black, J. M., Shimmings, P., & Owen, M. (1998). The spring range of barnacle geese *Branta leucopsis* in relation to changes in land management and climate. *Biological Conservation*, 86(3), 339–346. [https://doi.org/10.1016/s0006-3207\(98\)00029-9](https://doi.org/10.1016/s0006-3207(98)00029-9)
- Prop, J., & de Vries, J. (1993). Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. *Ornis Scandinavica*, 24(2), 110–121. <https://doi.org/10.2307/3676360>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reed, E. T., Gauthier, G., & Giroux, J.-F. (2004). Effects of spring conditions on breeding propensity of greater snow goose females. *Animal Biodiversity and Conservation*, 27(1), 35–46.

- Robinson, R. A., Crick, H. Q., Learmonth, J. A., Maclean, I., Thomas, C. D., Bairlein, F., ... Godley, B. J. (2009). Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, 7(2), 87–99. <https://doi.org/10.3354/esr00095>
- Ryder, J. P. (1970). A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.*, 82(1), 5–13.
- Sæther, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. *Trends in Ecology & Evolution*, 12(4), 143–149. [https://doi.org/10.1016/S0169-5347\(96\)10068-9](https://doi.org/10.1016/S0169-5347(96)10068-9)
- Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K. B., ... Dobson, F. S. (2013). How life history influences population dynamics in fluctuating environments. *The American Naturalist*, 182(6), 743–759. <https://doi.org/10.1086/673497>
- Sæther, B. E., Grøtan, V., Tryjanowski, P., Barbraud, C., Engen, S., & Fulin, M. (2006). Climate and spatio-temporal variation in the population dynamics of a long distance migrant, the white stork. *Journal of Animal Ecology*, 75(1), 80–90. <https://doi.org/10.1111/j.1365-2656.2005.01023.x>
- Sainmont, J., Andersen, K. H., Varpe, Ø., & Visser, A. W. (2014). Capital versus income breeding in a seasonal environment. *The American Naturalist*, 184(4), 466–476. <https://doi.org/10.1086/677926>
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., ... Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278, 835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Samelius, G., & Alisauskas, R. T. (2000). Foraging patterns of arctic foxes at a large arctic goose colony. *Arctic*, 53(3), 279–288. <https://doi.org/10.14430/arctic858>
- Schaub, M., Kania, W., & Köppen, U. (2005). Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology*, 74(4), 656–666. <https://doi.org/10.1111/j.1365-2656.2005.00961.x>
- Sedinger, J. S., & Raveling, D. G. (1986). Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *Journal of Animal Ecology*, 55(3), 1083–1102. <https://doi.org/10.2307/4435>
- Sedinger, J. S., Chamber, J. L., Ward, D. H., Nicolai, C. A., & Conant, B. (2011). Carryover effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. *The American Naturalist*, 178(5), E110–E123. <https://doi.org/10.1086/662165>
- Serreze, M. C., & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global Planetary Change*, 77(1–2), 85–96. <https://doi.org/10.1016/j.gloplacha.2011.03.004>
- Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling*, 7(2), 206–218. https://doi.org/10.1207/s15328007sem0702_4
- Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90(2), 363–368. <https://doi.org/10.1890/08-1034.1>
- Shipley, B. (2016). *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference with R*. Cambridge, UK: Cambridge University Press.
- Singmann, H., Bolker, B., & Westfall, J. (2015). afex: Analysis of factorial experiments. R package version 0.15-2. Retrieved from <http://CRAN.R-project.org/package=afex>
- Skinner, W., Jefferies, R., Carleton, T., Abraham, R. R., & Dagger, K. (1998). Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology*, 4(1), 3–16. <https://doi.org/10.1046/j.1365-2486.1998.00097.x>
- Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M. M. B., Allen, S. K., Boschung, J., ... Midgley, P. M. (2014). *IPCC 2013: Climate change 2013: The physical science basis: Working Group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, 22(11), 1–23. <https://doi.org/10.18637/jss.v022.i11>
- Trinder, M. N. (2014). Status and population viability of Svalbard barnacle geese in Scotland. *Scottish Natural Heritage Commissioned Report No.756*. Scottish Natural Heritage, Inverness, UK.
- Van der Jeugd, H. P., Eichhorn, G., Litvin, K. E., Stahl, J., Larsson, K., Van Der Graaf, A. J., & Drent, R. H. (2009). Keeping up with early springs: Rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology*, 15(5), 1057–1071. <https://doi.org/10.1111/j.1365-2486.2008.01804.x>
- Van der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass. *Ecology*, 95(12), 3414–3427. <https://doi.org/10.1890/14-0533.1>
- Van Eerden, M. (1996). The response of Anatidae to changes in agricultural practice: Long-term shifts in the carrying capacity of wintering waterfowl. *Gibier Faune Sauvage*, 13, 681–706.
- van Oudenhove, L., Gauthier, G., & Lebreton, J. D. (2014). Year-round effects of climate on demographic parameters of an arctic-nesting goose species. *Journal of Animal Ecology*, 83(6), 1322–1333. <https://doi.org/10.1111/1365-2656.12230>
- Van Wijk, R. E., Kölzsch, A., Kruckenberg, H., Ebbinge, B. S., Müskens, G. J., & Nolet, B. A. (2012). Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*, 121(5), 655–664. <https://doi.org/10.1111/j.1600-0706.2011.20083.x>
- Ward, D. H., Røstad, E. A., Sedinger, J. S., Lindberg, M. S., & Dawe, N. K. (1997). Seasonal and annual survival of adult Pacific brant. *The Journal of Wildlife Management*, 61(3), 773–781. <https://doi.org/10.2307/3802184>
- White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, 46(sup1), S120–S139. <https://doi.org/10.1080/00063659909477239>
- Williams, T., Cooch, E., Jefferies, R., & Cooke, F. (1993). Environmental degradation, food limitation and reproductive output: Juvenile survival in lesser snow geese. *Journal of Animal Ecology*, 62(4), 766–777. <https://doi.org/10.2307/5395>
- WWT. (2017). *WWT Svalbard Barnacle Goose*. Latest results. Retrieved from <http://monitoring.wwt.org.uk/our-work/goose-swan-monitoring-programme/species-accounts/svalbard-barnacle-geese/>
- Ydenberg, R. C., & Prins, H. H. T. (1981). Spring grazing and manipulation of food quality by Barnacle Geese. *Journal of Applied Ecology*, 18(2), 443–453. <https://doi.org/10.2307/2402405>

SUPPORTING INFORMATION

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

How to cite this article: Layton-Matthews K, Hansen BB, Grøtan V, Fuglei E, Loonen MJJE. Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. *Glob Change Biol.* 2020;26:642–657. <https://doi.org/10.1111/gcb.14773>