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RESEARCH ARTICLE

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Density-dependent population dynamics of a high Arctic capital breeder, the barnacle goose

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Abstract

1. Density regulation of the population growth rate occurs through negative feedbacks on underlying vital rates, in response to increasing population size. Here, we examine in a capital breeder how vital rates of different life-history stages, their elasticities and population growth rates are affected by changes in population size.
2. We developed an integrated population model for a local population of Svalbard barnacle geese, *Branta leucopsis*, using counts, reproductive data and individual-based mark–recapture data (1990–2017) to model age class-specific survival, reproduction and number of individuals. Based on these estimates, we quantified the changes in demographic structure and the effect of population size on age class-specific vital rates and elasticities, as well as the population growth rate.
3. Local density regulation at the breeding grounds acted to reduce population growth through negative effects on reproduction; however, population size could not explain substantial variation in survival rates, although there was some support for density-dependent first-year survival.
4. With the use of prospective perturbation analysis of the density-dependent projection matrix, we show that the elasticities to different vital rates changed as population size increased. As population size approached carrying capacity, the influence of reproductive rates and early-life survival on the population growth rate was reduced, whereas the influence of adult survival increased. A retrospective perturbation analysis revealed that density dependence resulted in a positive contribution of reproductive rates, and a negative contribution of the numbers of individuals in the adult age class, to the realised population growth rate.
5. The patterns of density dependence in this population of barnacle geese were different from those recorded in income breeding birds, where density regulation mainly occurs through an effect on early-life survival. This indicates that the population dynamics of capital breeders, such as the barnacle goose, are likely to be more reproduction-driven than is the case for income breeders.

KEYWORDS
barnacle geese, capital breeder, density dependence, integrated population model, perturbation analysis, population dynamics

1 | INTRODUCTION

Population dynamics are determined by a combination of density dependence and environmental stochasticity, acting through an influence on species' vital rates (Lande, Engen, & Saether, 2003; Turchin, 1995), thereby controlling the underlying mechanisms regulating and limiting population growth (Grant & Benton, 2000; Ricklefs, 1983). Consequently, density dependence has received much attention as a fundamental mechanism driving population dynamics (Lande et al., 2002; Ricklefs, 2000). Gaining a mechanistic understanding of how density dependence drives population fluctuations requires a consideration of demographic structure (Coulson et al., 2001; Lande et al., 2002). For long-lived species, the mechanisms through which density dependence acts are often largely determined by age-specific variation in life history (Fowler, 1981; Lande et al., 2002). For example, younger age classes may be more vulnerable to density-dependent effects (Gaillard & Yoccoz, 2003). Alternatively, older breeding individuals may be more resource demanding and hence can suffer more from resource competition (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Lok, Overdijk, Tinbergen, & Piersma, 2013). Ignoring this variation among age classes in their response to density can ultimately bias inferences about underlying processes affecting fluctuations in population size (Gamelon et al., 2016).

Accurately estimating the strength of density dependence therefore requires long time series of high-quality demographic data (Both, Visser, & Verboven, 1999; Coulson et al., 2001) as well as a robust modelling approach to analyse them, accounting for all potential sources of error (Freckleton, Watkinson, Green, & Sutherland, 2006; Shenk, White, & Burnham, 1998). A challenge in studies of population dynamics is access to data covering a sufficiently wide range of population sizes for obtaining unbiased estimates of density-dependent effects (Brook & Bradshaw, 2006). Populations establishing themselves in new areas represent a unique opportunity for analysing density-dependent processes (Nicoll, Jones, & Norris, 2003; Redfield, 1973). However, examples are few, since long-term studies tend to focus on well-established populations. Here, we take the rare advantage of analysing the dynamics of a high Arctic barnacle goose, *Branta leucopsis*, population that colonised Kongsfjorden, Svalbard, in the 1980s (Loonen, Tombre, & Mehlum, 1998; Owen, 1984). Barnacle geese are predominantly capital breeders, partly due to the unpredictability of environmental conditions at the high Arctic breeding grounds. Although the "degree of capital breeding" can vary, depending on environmental conditions (Hobson, Sharp, Jefferies, Rockwell, & Abraham, 2011), they utilise resources accumulated during the spring migration to initiate breeding (Hahn, Loonen, & Klaassen, 2011). The inter-annual environmental stochasticity in the high Arctic can lead to resource competition and potentially strong density-dependent effects (Bruggeman, Swem, Andersen, Kennedy, & Nigro, 2015).

In a comparative study of age-structured density-dependent effects in other bird species, Sæther et al. (2016) revealed a remarkably simple pattern. They found that density dependence mainly acted through an influence on survival, especially during the first year. Furthermore, the relative influence of survival rates of older individuals on the population growth rate, expressed by the elasticity (Caswell, 2001), increased when population size approached carrying capacity. However, the generality of these findings still remains uncertain because all species included in the analyses can be characterised as income breeders to varying degrees (Durant, Massemin, Thouzeau, & Handrich, 2000; Meijer & Drent, 1999), where energy required for reproduction is acquired at the breeding grounds (Drent & Daan, 1980).

We examine how variation in population size affects different vital rates of the capital breeding barnacle geese. This high Arctic migrant must bring sufficient amounts of endogenous reserves to the breeding grounds to meet the energetic requirements for egg laying and incubation (Hahn et al., 2011). Using 28 years (1990–2017) of population counts and individual-based mark–recapture data from a local population in Svalbard, we develop an integrated population model (IPM (Abadi, Gimenez, Arlettaz, & Schaub, 2010; Schaub & Abadi, 2011)) to investigate patterns of density regulation and changes in demographic rates and age structure. By parameterising a post-breeding, age-structured population projection matrix, we quantify the elasticities of the population growth rate to density-dependent demographic rates across a range of population sizes, using a prospective perturbation analysis (Caswell, 2001). We also quantify the contributions of vital rates and population structure to the realised population growth rate, using a transient retrospective perturbation analysis (Caswell, 2007; Koons, Iles, Schaub, & Caswell, 2016).

2 | MATERIALS AND METHODS

2.1 | Study species and site

The study population of barnacle geese breed and rear their young in Kongsfjorden, Svalbard, close to the settlement of Ny-Ålesund (78°55'N, 11°56'S). They are long-lived birds (up to 28 years) and form monogamous breeding pairs. During the summer breeding season (May to September), they breed on islands in the fjord and rear their young along the coastline later in the season. Successful breeding pairs lay a single clutch of three to five eggs on average during June and offspring fledge in August (Owen & Black, 1989). The total flyway Svalbard population winters at Solway Firth, UK, and migrates to breeding sites across Svalbard in summer, via spring staging areas along the coast of mainland Norway.

2.2 | Data collection

Following their colonisation in the 1980s, a local mark–recapture programme was initiated in 1990 where individuals are caught and marked with unique colour bands and metal identification rings. Sex is determined by cloacal inspection and behavioural observations (Loonen, Oosterbeek, & Drent, 1997). Although fledglings are clearly distinguishable from older birds, thereafter the difference is difficult to determine and therefore only individuals of known age (i.e. marked as fledglings) were included in the survival analysis, which was age class-dependent. Re-sightings of marked birds take place twice per day in the area around Ny-Ålesund, and catches take place at least twice during a season. Data on reproduction are recorded on the two main nesting islands during the hatching phase; nests are visited on the islands at one- to two-day intervals to record the number of goslings, and families are followed throughout the season to determine the number of fledglings per breeding pair at the end of the season in August.

Count data of the number of yearlings and adults in Kongsfjorden came from two sources; from 1990 to 1996, total population size was estimated from the number of marked individuals observed, divided by the average proportion of marked geese in catches, known as a Petersen estimate (Begon, 1979). After 1996, counts of the number of yearlings and adults occurred during the moulting phase (end of July). Only counts of yearlings and adults (combined) were included since the timing of counts was often before first-year birds fledged and pre-fledging mortality is high (Loonen et al.,1998).

2.3 | Integrated population model

The mark–recapture dataset used for this analysis consisted of 3,487 individuals, marked between 1990 and 2017. Using an integrated population model framework (Abadi, Gimenez, Arlettaz, et al., 2010), we simultaneously analysed mark–recapture, reproduction and population count data. Based on the life cycle of the barnacle goose (Figure 1), we developed age-structured, post-breeding state equations with three age classes (fledglings, yearlings and adults) to estimate the annual probability of reproduction, *R*, fecundity, fec and age class-specific (apparent) survival $\phi_{\mathrm{a}\supset \mathrm{f,y,ad}}$, (Figure 2b,c). Reproductive rates, *R* and fec, determine the number of fledglings produced in August, the first survival rate for the fledgling age class describes survival in the first year of life, from August at year *t* to August at year *t* + 1, the yearling age class to the second year and adults from the third year onwards.

Mark–recapture data were analysed as individual capture histories and modelled with a Cormack–Jolly–Seber model (Lebreton, Burnham, Clobert, & Anderson, 1992). Survival parameters were estimated as functions of time and age, from year *t* to *t* + 1 and for fledglings (ϕ_{f}), yearlings (ϕ_{y}) and adults (ϕ_{ad}). Apparent survival was modelled on the logit scale, with a Bernoulli distribution, and varied with age (a) and year (*t*); $\mathrm{logit}\,(\phi_{a,t+1}) = \mu_{\phi_a} + \varepsilon_{\phi_{a,t+1}}$. We found no difference in survival between sexes, but the recapture rate of females (0.62; 0.56, 0.67) was higher than that of males (0.41; 0.36, 0.47), as a consequence of higher philopatry in females (Black, Prop, & Larsson, 2014).

Reproductive data of the annual number of fledglings produced, for the female portion of the population, were defined by two parameters describing reproduction at year *t* + 1 (*R* and fec). *R* was the annual probability of a female producing at least one fledgling, and fec was the average number of fledglings per successfully breeding female. Reproduction was considered from the second year of life and was independent of age. The probability that a female produces at least one fledgling (*R*) was modelled with a Bernoulli distribution, where $\mathrm{logit}\,(R_{t+1}) = \mu_R + \varepsilon_{R,t+1}$. The number of fledglings per successfully breeding female (fec) was modelled with a Poisson distribution, where $\log\,(\mathrm{fec}_{t+1}) = \mu_{\mathrm{fec}} + \varepsilon_{\mathrm{fec},\,t+1}$. Annual reproduction at year *t* + 1 was therefore the product of breeder survival $\phi_{\mathrm{a},t}$, the probability of reproduction R_{t+1}, the number of fledglings per successfully breeding female fec_{t+1} and 0.5, assuming an equal offspring sex ratio, since reproductive rates were only based on females.

To account for a potential correlation in environmental effects on vital rates, we modelled the temporal variance in ϕ_{a}, *R* and fec assuming that the variance originated from a random process with a mean of zero, but with vital rate- and age class-specific deviations (Schaub, Jakober, & Stauber, 2013). Ɛ is a matrix of the temporal residuals for each rate, as described by Link and Barker (2005). Temporal residuals were treated as a realisation from a multivariate normal distribution (MVN) with zero mean, $\varepsilon \sim \mathrm{MVN}(0, \Sigma)$, where Σ is the variance–covariance matrix (Schaub et al., 2013), with the scaled inverse Wishart distribution as the prior for Σ (Gelman & Hill, 2006, p.286). With this approach, we estimated the temporal variance of each parameter and the covariances between parameters as the sub-diagonals of the matrix. Since the recapture probability was not expected to be correlated with vital rates, the temporal variance was modelled independently with a fixed effect of sex (*s*) and a random effect of year (*t*); $\log\mathrm{it}\,(p_{s,t+1}) \sim \mathrm{Normal}\,(\mu_{p,s},\, \sigma^2_{p,t+1})$.

The state process equations model the annual expected numbers of individuals in each age class, based on the underlying demographic rates. We modelled reproduction into the first age class as a Poisson process and survival to subsequent age classes as Binomial processes to incorporate demographic stochasticity (Lande et al., 2003). The model describing the number of individuals in each class at year *t* + 1 can be written as.

$$N_{\mathrm{f}_{t+1}} \sim \mathrm{Poisson}\,(R_{t+1}\,\mathrm{fec}_{t+1}(N_{\mathrm{y}_t}\phi_{\mathrm{y}_t} + N_{\mathrm{ad}_t}\phi_{\mathrm{ad}_t})/2), \tag{1}$$

$$N_{\mathrm{y}_{t+1}} \sim \mathrm{Binomial}\,(\phi_{\mathrm{f}_t}, N_{\mathrm{f}_t})\ \text{and} \tag{2}$$

$$N_{\mathrm{ad}_{t+1}} \sim \mathrm{Binomial}\,(\phi_{\mathrm{y}_t}, N_{\mathrm{y}_t}) + \mathrm{Binomial}\,(\phi_{\mathrm{ad}_t}, N_{\mathrm{ad}_t}). \tag{3}$$

Estimating the number of unmarked individuals entering the marked population is important for correctly estimating vital rates,

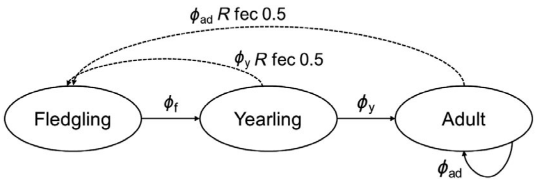

FIGURE 1 Age class-structured life cycle of the barnacle goose based on fledgling (f), yearling (y) and adult (ad) age classes. ϕ_{a} is the probability of an individual in age class *a* surviving to the next year, *R* is the probability of a female producing a fledgling and fec is the number of fledglings per successful female breeder. Age class-specific contributions to reproduction are based on breeder survival (ϕ_{y} or ϕ_{ad}), *R* and fec, multiplied by 0.5 to account for sex ratio, in accordance with a post-breeding census

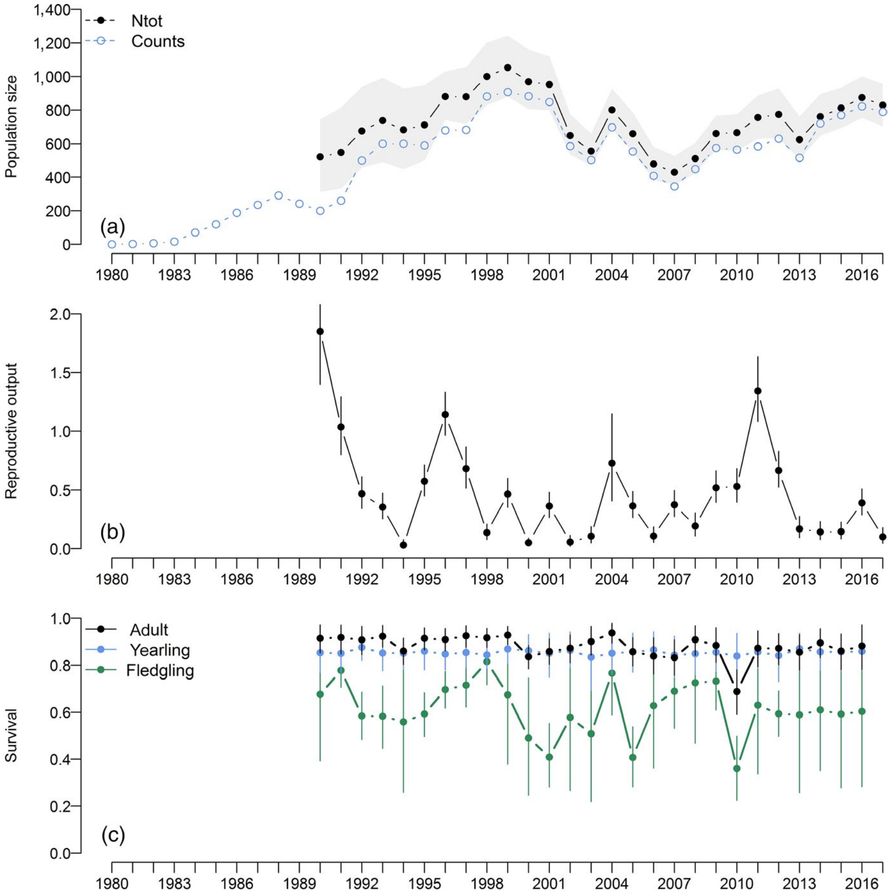

FIGURE 2 (a) Model estimates of total population size from 1990 to 2017 (black) with 95% CRIs (grey shading). Population count data are shown based on counts of nests in Kongsfjorden from 1980 to 1990 (Fuglei, Øritsland, & Prestrud, 2003), on a Petersen index from 1990 to 1996 (see Methods) and total fjord counts of the number of yearlings and adults in Kongsfjorden from 1996 to 2017. The consistent discrepancy between model estimates and total counts is due to the exclusion of fledglings from total counts. (b) Posterior means and 95% CRIs of the reproductive output (product of *R* and fec). (c) Annual estimates of age class-specific survival rates (ϕ_f, ϕ_y and ϕ_{ad})

but can be challenging in demographic studies (Schaub, Aebischer et al. 2010, Lieury, Gallardo et al. 2015). Changes in the numbers of unmarked birds in the study area were accounted for by estimating the annual proportion of unmarked fledglings and older birds (Abadi, Gimenez, Ullrich, Arlettaz, & Schaub, 2010). We estimated the rate of addition of unmarked fledglings (U_f) and older birds ($U_{y,ad}$). This allows unmarked individuals to enter the population at each time step, assuming the same vital rates as marked individuals. The numbers of unmarked fledglings (N_{U_f}) and older birds ($N_{U_{y,ad}}$) were modelled as a Poisson process;

$$N_{U_{f_{t+1}}} \sim \text{Poisson}\,(N_{f_t} U_{f_t}) \text{ and} \tag{4}$$

$$N_{U_{y,ad_{t+1}}} \sim \text{Poisson}\,\left(\left(N_{y_t}+N_{ad_t}\right) U_{y,ad_t}\right), \tag{5}$$

where N_f, N_y and N_{ad} correspond to the numbers of marked fledglings, yearlings and adults, and N_{U_f} and $N_{U_{y,ad}}$ to the number of unmarked fledglings and older birds (yearlings and adults). We calculated the annual total number of marked and unmarked birds, N_{tot}, by summing N_f, N_y, N_{ad}, N_{U_f} and $N_{U_{y,ad}}$.

We modelled annual population counts using a state-space model, which combines the state process model, describing the true state of the system, with an observation process model (de Valpine & Hastings, 2002). Total counts were available for yearlings and adults; however, counts of fledglings (C_{f,c_t}) were not available, since total fjord counts often took place before fledging in August (see Section 2.2). Therefore, C_{f,c_t} was included as a matrix of NAs and estimated as a latent variable. We assumed a log-normal distribution for the population count data and the variance in the observation probability was assumed to differ for the period where counts were based on a Petersen index (1990–1996) and the period where total fjord counts were conducted (1997–2017). The observation model links the counts ($C_{a,c,t}$) to the latent population numbers by;

$$\log\left(C_{f,c_t}\right) \sim \text{Normal}\left(\log\left(N_{f_t}+N_{U_{f_t}}\right), \sigma^2_{C_c}\right) \tag{6}$$

for fledglings and

$$\log\left(C_{y,ad,c_t}\right) \sim \text{Normal}\left(\log\left(N_{y_t}+N_{ad_t}+N_{U_{y,ad_t}}\right), \sigma^2_{C_c}\right) \tag{7}$$

for yearlings and adults, where the variance in $\sigma^2_{C_c}$ represents the observation error for counts estimated using the Petersen index or the total fjord counts (*c*). The combined likelihood of the state and observation process models is therefore given by; $L_{sp}(N \mid \phi, R, \text{fec}) \times L_{ob}(C \mid N, \sigma^2_{C_c})$.

The IPM was implemented in a Bayesian framework with non-informative priors (see Appendix S1). Posterior distributions of parameters were obtained using Markov Chain Monte Carlo simulations, implemented in JAGS (Plummer, 2003) via the program JAGSUI, version 1.4.4 (Kellner, 2015), in R version 3.4.0 (Team, 2017). Four separate chains were run for 1,000,000 iterations, with a burn-in of 100,000 iterations and thinning every 90th sample, resulting in 40,000 posterior samples from which posterior means and 95% Bayesian credible intervals (CRIs) were estimated. Convergence was assessed by ensuring $\hat{R}$ values for each parameter were less than 1.1 (Brooks & Gelman, 1998).

2.4 | Density dependence

We conducted post hoc linear regressions to estimate the effect of population size on vital rates and the population growth rate, using the 40,000 posterior samples of vital rates and population sizes from the IPM analysis, similar to Schaub et al. (2013). We regressed the logit of age class-specific survival (ϕ_a) at year t to $t + 1$ against total numbers of individuals (N_{tot}) at year t, to approximate the strength of density dependence on survival. The logit of the probability of reproduction (R) and the log of fecundity (fec) at year t were regressed against the annual numbers of yearlings and adults ($N_{y,ad}$). We formulated linear equations describing the strength of density regulation on ϕ_a, R and fec, where the intercept of each regression corresponds to the mean of each demographic rate, the regression coefficient to the strength of density dependence and the residuals to the remaining variance not explained by density. We regressed the population growth rate (λ) on total numbers of individuals (N_{tot}), to assess whether there was a net effect of density on population growth. We also tested for a temporal trend in vital rates and age class-specific numbers by fitting a linear regression with a continuous year effect. We also conducted density-dependent regressions with a continuous year effect, to ensure that any negative effects of density dependence on vital rates were not caused by temporal trends. Regression coefficients were estimated for all 40,000 posterior samples, from which mean and 95% CRIs were calculated, as well as the probability of the coefficients to be less than zero ($P(\beta < 0)$).

2.5 | Population dynamics

We parameterised an age-structured, post-breeding population projection matrix based on the state process equations. The asymptotic population growth rate (λ) was approximated as the maximum eigenvalue, and reproductive values and the stable age distribution were approximated as the left and right eigenvalues, respectively, of the projection matrix, using each sample of vital rates from the posterior distribution to calculate means and 95% CRIs (Caswell, 2001). We adopted an asymptotic prospective perturbation analysis, to quantify the sensitivity of λ to a proportional change (elasticity) in each demographic rate (Caswell, 2000).

Short-term, transient dynamics can differ from asymptotic dynamics, particularly in highly stochastic environments, influencing population dynamics through feedbacks between vital rates and population structure (Koons et al., 2016; Stott, 2016). We performed a transient prospective perturbation analysis to calculate the transient elasticities of the population vector (N_t) to lower-level vital rates (Caswell, 2007). We also performed a transient retrospective analysis (LTRE) (Koons, Arnold, & Schaub, 2017; Koons et al., 2016), to determine the contributions of vital rates and population structure to the realised population growth rate, $\lambda_{realised,t}$ (Appendix S6).

Demographic rates were predicted over the observed range of total population sizes using the regression coefficients described in the previous section, to determine how density dependence influenced the sensitivity and elasticity of λ to each demographic rate. Since some matrix elements were the product of multiple demographic rates, we calculated the elasticity of λ to each demographic rate (lower-level elasticities) analytically, by differentiation of each matrix element with respect to the parameter and application of the chain rule (Caswell, 2000). Sensitivities and elasticities were calculated using the 40,000 posterior samples of the regression coefficients and demographic rates, at a hundred population sizes, ranging from the minimum to maximum estimated N_{tot}. This resulted in 40,000 sensitivity and elasticity estimates for each demographic rate, which were used to calculate means and 95% CRIs.

3 | RESULTS

3.1 | Temporal trends in population size and structure

Following their colonisation of the breeding grounds in Kongsfjorden, western Svalbard, the estimated population size grew from 521 individuals (95% CRIs: 314, 745) in 1990 to a maximum of 1,054 (881, 1,244) individuals in 1999, before fluctuating around 700 individuals (Figure 2a). The number of fledglings, N_f, (slope = −1.33; CRI = −2.02, −0.55) and yearlings, N_y, (−1.28; −2.09, −0.41) declined, and the probabilities of the regression slopes being negative were both 1.00 ($P(\beta < 0)$). This decline was largely driven by the first and last years of the study. The number of adults, $N_{ad,}$ increased (9.38; 6.25, 12.10), and the probability of this slope being positive was 1.00, indicating an ageing population (Appendix S3: Figure S3.1). The numbers of unmarked fledglings in the population (N_{U_f}) also showed a tendency for a negative trend (−2.45; −6.37, 1.22) where the probability of a negative slope was 0.89. The number of unmarked yearlings and adults ($N_{U_{y,ad}}$) increased over the study period (8.80; 5.49, 12.68), and the probability of this slope being positive was 1.00 (Appendix S3: Figure S3.2).

3.2 | Age class-specific demographic rates

The mean probability of an adult female (i.e. older than one year) breeding successfully (R) was 0.13 (0.09, 0.17), and the mean number of fledglings per successfully breeding female (fec) was 2.12 (1.85, 2.44). R (logit scale) showed a tendency for a decline over time (−0.0029; −0.0119, 0.0063); however, credible intervals overlapped 0 and the probability of the slope being negative was 0.70. fec (log scale) declined over time (−0.0111; −0.0160, −0.0046), where the probability of a negative slope ($P(\beta < 0)$) was 1.00. The temporal variance of R was larger than fec, and fledgling survival (ϕ_f) had a larger variance than survival of older age classes (Figure 3). Covariances between survival rates were generally positive, and R was positively correlated with ϕ_{ad}, although credible intervals overlapped 0 (Figure 3). We calculated the

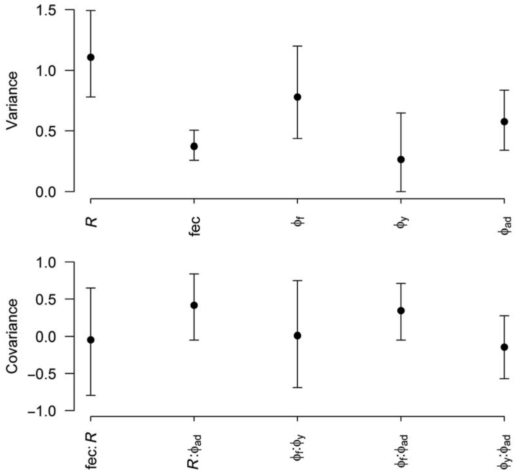

FIGURE 3 Mean parameter estimates of temporal variance and covariance in *R*, fec, ϕ_f, ϕ_y and ϕ_ad, with associated 95% CRIs

product of *R* and fec as a measure of annual reproductive output (per mature female), which declined rapidly in the first years of the study and was close to 0 in 1994, 2000 and 2002 (Figure 2b). As is typical in long-lived species, mean adult and yearling survival were high while fledgling survival was lowest (Table 1). The covariance between fledgling and adult survival was larger than yearling and adult survival, with a probability of 0.79 $\left(P\left(\mathrm{cov}(\sigma_f^2,\sigma_\mathrm{ad}^2) > \mathrm{cov}(\sigma_y^2,\sigma_\mathrm{ad}^2)\right)\right)$. Fledgling and yearling survival co-varied to a lesser extent $\left(P\left(\mathrm{cov}(\sigma_f^2,\sigma_y^2) < \mathrm{cov}(\sigma_y^2,\sigma_\mathrm{ad}^2)\right) = 0.58; P\left(\mathrm{cov}(\sigma_f^2,\sigma_y^2) < \mathrm{cov}(\sigma_f^2,\sigma_\mathrm{ad}^2)\right) = 0.83\right)$. Survival of adults (−0.024; −0.034, −0.013) and yearlings (−0.004; −0.015, −0.002) declined from 1990 to 2017, and fledgling survival (−0.008; −0.028, 0.022) showed a tendency for decline; however, credible intervals overlapped 0 and the probability of a negative slope was 0.75, compared to 0.91 and 1.00 for yearling and adult survival, respectively (Figure 2c).

3.3 | Density regulation at the breeding grounds

The number of yearlings and adults in Kongsfjorden had a negative effect on the probability of reproduction (*R*) and the number of fledglings per successfully breeding female (fec) (Table 1). This translated into a direct, negative effect of total population size on the population growth rate. No statistically significant negative effect of local density on survival was observed, although there was a tendency for a negative effect on fledgling survival (Table 1). The estimated density dependence coefficients were similar when temporal trends in vital rates and population size were accounted for (Appendix S5).

3.4 | Age-structured population dynamics

The mean population growth rate over the study period was 1.05 (0.65, 1.53). However, annual population growth rates showed large variation from 0.68 (0.54, 0.85) in 2001, the year prior to a major crash in reproductive success, to 1.27 (0.79, 1.73) in 1991, during the growth phase after colonisation. The stable age distribution of fledglings, yearlings and adults, based on mean vital rate estimates, was 0.04 (0.02, 0.05), 0.03 (0.02, 0.04) and 0.94 (0.92, 0.96), respectively, indicating that individuals were mostly distributed in the adult age class. Adult and yearling classes had the highest reproductive values, 0.94 (0.92, 0.97) and 0.92 (0.87, 0.97), respectively, vs. 0.67 (0.55, 0.75) for the fledgling age class.

Mean sensitivities and elasticities of the asymptotic population growth rate (λ) to vital rates were calculated from a population projection matrix based on posterior samples of age-specific demographic rates. The mean sensitivity of λ to the probability of reproduction (*R*) was higher than to the number of fledglings (fec), while the elasticities of λ to *R*, fec and ϕ_f were the same (Table 1). The sensitivity and elasticity of λ to variation in survival were substantially higher for the rate of the adult age class than for the survival rates of yearlings and fledglings, which were not statistically significantly different (Table 1).

We parameterised population projection matrices where vital rates were functions of population size (Caswell, 2001), based on density dependence coefficients for each vital rate. Elasticities of the population growth rate to *R*, fec, ϕ_f and ϕ_y were consistently lower than ϕ_ad and declined with population size at the same rate (Figure 4a). Conversely, the elasticity to ϕ_ad increased as the population approached the carrying capacity.

Transient elasticities of the population vector at t = 5, $N_{5,}$ rapidly converged to the same pattern as in the asymptotic elasticities, with increasing elasticity to adult survival and decreasing elasticities to other vital rates as population size increased (Appendix S6: Figure S6.1). Based on the transient LTRE, contributions of vital rates to the realised population growth rate, $\lambda_{\mathrm{realised},t}$, reflected the strength of density dependence acting on each rate (since reproductive rates were negatively affected by N_tot, reproductive rates made a positive contribution to $\lambda_{\mathrm{realised},t}$) (Figure 4b). Additionally, the population vector reduced population growth through a negative effect on the number of adults, which made up the largest proportion of total population size.

4 | DISCUSSION

Colonising populations should eventually stop increasing as a consequence of density dependence in certain vital rates (Redfield, 1973). However, few studies of colonising populations – particularly in migratory species – have identified which age-specific reproductive and survival rates undergo density regulation and how this in turn affects the population dynamics (Fowler, 1981, 1987). Sæther et al. (2016) found no evidence for density regulation of reproduction, when analysing density dependence in different vital rates of income breeding birds. In contrast, density regulation in several duck species, which are closer to being capital breeders, was found to occur primarily through negative feedbacks on reproduction (Elmberg, Gunnarsson, Nummi, Pöysä, & Sjöberg, 2003; Elmberg, Gunnarsson, Pöysä, Sjöberg, & Nummi, 2005). Similarly, in our study population of barnacle geese and in other

TABLE 1 Estimates of population growth rate λ and demographic rates at mean population size, with corresponding sensitivities and elasticities of the population growth rate and coefficients (β) describing the effect of N (local population, i.e. the total population size N_{tot} or the numbers of yearlings and adults $N_{y,ad}$) on demographic rates, with associated 95% credible intervals. Coefficients describing the strength of density dependence, fec and λ were distributed on the log scale, while R, ϕ_f, ϕ_y and ϕ_{ad} were distributed on logit scale

Par	Mean	Sensitivity of λ	Elasticity of λ	N	β on link scale (×10^3) (95% CRIs)	$P(\beta < 0)$)
R	0.13 (0.09 0.17)	0.21 (0.17, 0.24)	0.03 (0.02, 0.04)	$N_{y,ad}$	−1.73 (−2.61, −0.75)	1.00
fec	2.12 (1.85, 2.44)	0.04 (0.02, 0.06)	0.03 (0.02, 0.04)	$N_{y,ad}$	−0.48 (−0.84, −0.13)	1.00
ϕ_f	0.63 (0.53 0.72)	0.04 (0.03, 0.06)	0.03 (0.02, 0.04)	N_{tot}	−0.04 (−1.36, 1.25)	0.52
ϕ_y	0.86 (0.82 0.90)	0.03 (0.02, 0.04)	0.03 (0.02, 0.04)	N_{tot}	0.03 (−0.60, 0.73)	0.46
ϕ_{ad}	0.89 (0.87 0.91)	0.97 (0.96, 0.98)	0.94 (0.92, 0.96)	N_{tot}	0.41 (−0.34, 1.20)	0.14
λ	1.05 (0.65, 1.53)			N_{tot}	−0.54 (−0.81, −0.36)	1.00

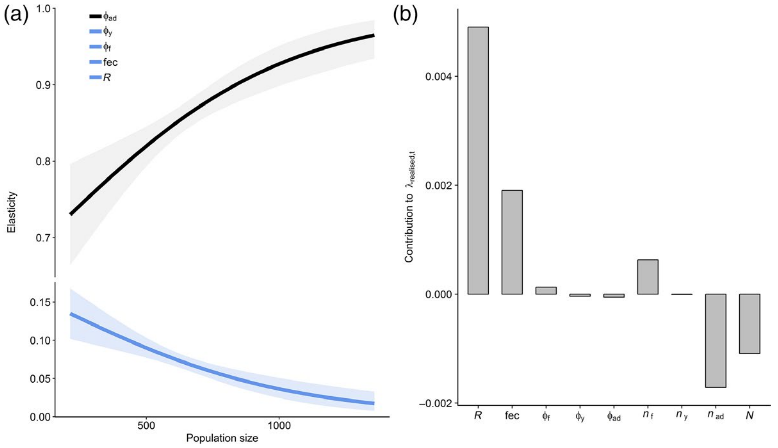

FIGURE 4 (a) Elasticities of the asymptotic population growth rate to vital rates, in relation to total population size, with 95% CRIs. Elasticities to R, fec, ϕ_f and ϕ_y were the same, and consequently, lines are overlapping. (b) Contributions of demographic rates and normalised components of the population structure to the realised population growth rate, $\lambda_{realised,t}$

goose species (Cooch, Lank, Rockwell, & Cooke, 1989; Sedinger et al., 1998), density dependence largely regulated population growth via a negative feedback on reproductive success prior to fledging.

A central concept in classifying reproductive tactics is the capital–income dichotomy, which separates species where reproductive success relies on body stores (capital) from species that invest in offspring using resources directly at the breeding grounds (Drent & Daan, 1980; Jönsson, 1997; Stearns, 1992). Analyses of ungulates have revealed that the pattern of temporal covariation in demographic traits differs between those two life-history types. In capital breeders such as bighorn sheep (*Ovis canadensis*), ewes successfully weaning a lamb were heavier than those losing their lamb (Festa-Bianchet, Gaillard, & Jorgenson, 1998), whereas in the income breeding roe deer (*Capreolus capreolus*), there was no detectable difference in female body mass between years with successful and unsuccessful fawn production (Andersen, Gaillard, Linnell, & Duncan, 2000). Waterfowl, such as geese and ducks, are closer to the capital breeding end of the spectrum, in which the endogenous nutrients brought to the breeding grounds may affect their reproductive success (Hahn et al., 2011; Klaassen, Abraham, Jefferies, & Vrtiska, 2006). This indicates that population dynamics of capital breeders, such as barnacle geese, can be characterised by a "tap-type", rather than a "tub-type", of dynamics (Sæther et al., 2006; Sæther, Sutherland, & Engen, 2004), that is processes influencing the mean body condition prior to the breeding season affect reproductive success and hence strongly affect population dynamical characteristics.

In this study, we found strong support for density dependence acting through a negative feedback on reproduction. Stronger density regulation of reproduction than survival in barnacle geese may therefore be explained by their status as capital breeders, with processes during the breeding season making a larger contribution to population dynamics. In contrast, Sæther et al. (2016) found that annual variation in population growth rates of income breeding bird species was mainly explained by temporal variation in survival. In addition, barnacle geese are also nidifugous (i.e. offspring leave the nest shortly after hatching and receive minimal parental care thereafter) in contrast to altricial species, where offspring hatch in an undeveloped state (Lack, 1968). Sæther, Ringsby, and Røskaft (1996) proposed that factors affecting the population dynamics of nidifugous species would occur during the breeding season, but would occur during the non-breeding season in altricial species. Consequently, the vulnerability of barnacle goose young to fluctuations in the availability of food resources may be greater than in altricial species. In support of this, the majority of species included in the analysis of Sæther et al. (2016) were altricial birds. Furthermore, studies have shown that herbivores in particular are strongly affected by environmental stochasticity and density dependence, which often acts through density regulation of reproduction since the temporal variance in adult survival is limited (Gaillard et al., 1998; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Sæther, 1997). This pattern may therefore be especially clear in herbivores since their body condition is strongly dependent on the amount of food available prior to or during a season. In our study, population density influenced both the probability of reproduction and the number of fledglings, conditional on successful reproduction. Such density effects may be attributed to competition for food resources prior to the breeding season, with consequent carry-over effects on reproduction (Sedinger, Schamber, Ward, Nicolai, & Conant, 2011). Additionally, density-dependent reproduction is likely also explained by competition for nest sites and/or food resources during the brood rearing phase, where increased food competition at the breeding grounds has been linked to higher prefledging mortality in barnacle geese (Larsson & Forslund, 1994; Loonen et al., 1997). Finally, the number of Arctic foxes in Kongsfjorden has increased in parallel with goose numbers, affecting reproduction directly through predation but also indirectly by limiting available foraging area and exacerbating resource competition (Loonen et al.,1998).

In this population, survival appeared to be density-independent after the first year of life. Food conditions can influence both reproduction and survival in high Arctic geese through effects on body condition (Newton, 1977), which is a known determinant of survival in geese, since fat build-up is paramount to successful migration (Loonen et al., 1997; Newton, 1977). Both reproduction and survival showed a tendency for decline over the study period. Vital rates are typically high during the growing phase of a colonising population (Redfield, 1973), and this decline could be attributed to gradual habitat deterioration at the breeding grounds (Kuijper, Ubels, & Loonen, 2009) or by processes at other migratory stages. The continued increase in the total Svalbard flyway population, which convenes at the wintering grounds, may potentially also explain the decline in survival rates. No evidence of this was found when regressing age-specific survival rates against annual total population size, accounting for a linear temporal trend. However, we cannot rule out that this substantial linear increase in the Svalbard flyway population is, at least in part, responsible for the concomitant decline observed in local survival rates. When the year 1990 was removed from the analysis of density dependence (Appendix S5.2), we did find some support for density-regulated fledgling survival ($P(\beta < 0)) = 0.93$), potentially caused by post-fledging mortality during the first migration attempt, for example driven by food availability at the breeding grounds (Owen & Black, 1989). Similarly, in lesser snow geese, deteriorating food conditions was the main driver of increased first-year mortality (Francis, Richards, Cooke, & Rockwell, 1992). Therefore, density dependence may also act on fledgling survival by determining their first migration success, through limited resources at the breeding grounds. Deteriorating conditions and increased competition could also increase the amount of permanent emigration to other breeding grounds (causing a decline in apparent survival), rather than direct mortality, but we could not differentiate between these processes in the survival analysis.

Similar to Sæther et al. (2016), the elasticity of the population growth rate to adult survival increased as the population approached its carrying capacity. At small population sizes, the relative influence of reproductive rates and early-life survival on λ was high, but it declined with increasing population size. This is in agreement with Lack's hypothesis (1954; 1966) that, when a population is far from its carrying capacity, the system is driven by reproduction to a greater extent. However, Lack (1966) also argued that variation in reproduction should be largely independent of density, whereas in our study, population reproduction was strongly density-dependent. This discordance could stem from the aforementioned differences between income and capital breeders, which may alter the critical annual phase driving population dynamics (Sæther et al., 2004; Vander Werf, 1992). Thus, our analysis follows what would be predicted by Lack's hypothesis (1954) that, although reproductive rates vary as a density-dependent consequence of fluctuations in resources during the breeding season, the dynamics are still strongly influenced by adult survival as the population approaches its carrying capacity.

The elasticities of the population growth rate to demographic rates were typical for a long-lived species, where elasticities to reproductive rates and early-life survival are lower than to adult survival (Gaillard et al., 1998; Gaillard & Yoccoz, 2003). Survival often increases with age during the first few years of life in long-lived species, and such a pattern has also been observed for reproduction in geese (Rockwell, Cooch, Thompson, & Cooke, 1993). However, reproductive rates could not be modelled as age dependent in our study. Reproductive output also varied greatly among years in this barnacle goose population. This is a common pattern observed in several species of waterfowl, where elasticities to survival are high and reproduction tends to be more labile to environmental variation, allowing reproductive rates to contribute more to population dynamics (Koons, Gunnarsson, Schmutz, & Rotella, 2014). We have shown that in addition to the effects of environmental variation, the variability in reproductive rates can also be caused by density-dependent feedbacks. The large contribution of reproductive rates to population dynamics is also expected for long-lived birds with high survival rates and long life spans where, despite the low elasticity of λ to reproductive rates, their variance allows them to contribute substantially to realised population growth (Cooch, Rockwell, & Brault, 2001; Koons et al., 2014). The inter-annual variation was greater in the probability of producing a fledgling than in the number of fledglings per successful breeder, possibly since weather conditions influence initial nest success to a greater extent than the actual number of young (Prop & de Vries, 1993). Transient analysis can potentially reveal much about population dynamics in such variable environments (Ezard et al., 2010; Koons et al., 2017, 2016). In this case, the similarities between transient vs. asymptotic elasticities and contributions may be attributable to (a) the fact that vital rates were predicted deterministically as functions of vital rate-specific density dependence and (b) that this population reached the carrying capacity so quickly. Consequently, transient dynamics rapidly resembled asymptotic dynamics.

Understanding how density dependence influences the population dynamics and population trajectories of local populations colonising high Arctic breeding grounds is essential for their management and conservation, locally and internationally. This study gives insight into the dynamics behind the rapid expansion of migratory birds across the Arctic, currently a topic of management interest (AEWA, 2018; Trinder, 2014). These findings appear to oppose a recent study of the total flyway population of Svalbard barnacle geese at the wintering grounds, where no evidence of density regulation was observed (Trinder, 2014). Such a disparity can occur because density dependence in the total flyway population is concealed by range expansion on Svalbard, that is is only observable at a local scale. However, the limits of future range expansion are difficult to predict as climate change alters the area of suitable habitat for geese in the Arctic (Jensen et al., 2008; Post et al., 2009). The discrepancy between local and total Svalbard population dynamics indicates that, by ignoring local patterns, managers may miss changes occurring in Arctic migrant goose populations. Local density regulation can be seen as an early warning signal for future limitation of total flyway populations, when range expansion is no longer possible. We emphasise the need for a greater focus on local population dynamics and the suitability of remaining habitat at the high Arctic breeding grounds, especially when the re-introduction of hunting of migratory geese wintering in Europe is being called into question (AEWA, 2018).

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AUTHORS' CONTRIBUTIONS

K.L.M., B.B.H. and V.G. conceived the ideas and designed the methodology; M.L. collected the data; K.L.M., V.G. and C.C. analysed the data; and K.L.M., B.B.H. and B.E.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

R code for fitting the integrated population model and data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.200pk95 (Layton-Matthews, Loonen, Hansen, Coste, Sæther, & Grøtan, 2019).

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SUPPORTING INFORMATION

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

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