eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

1

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

2

herbivore

3

4

Kate Layton-Matthews[1], Vidar Grøtan[1], Brage B. Hansen[1], Maarten J. J. E. Loonen[2], Eva

5

Fuglei[3], Dylan Z. Childs[4]

6

[1]kate.l.matthews@ntnu.no, vidar.grotan@ntnu.no, brage.b.hansen@ntnu.no

7

[2]m.j.j.e.loonen@rug.nl

8

[3]eva.fuglei@npolar.no

9

[4]d.childs@sheffield.ac.uk

10

11

[1]Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science

12

and Technology, Trondheim, Norway

13

[2]Arctic Centre, University of Groningen, Groningen, the Netherlands

14

[3]Norwegian Polar Institute, Tromsø, Norway

15

[4]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

16

17

Corresponding author:

18

Kate Layton-Matthews

19

+47 941 565 75

20

kate.l.matthews@ntnu.no

21

22

Number of words: abstract = 149, main text = 4984, references = 89, figures = 4, tables = 2

23

24   **Running title:** population-growth responses to declining mass

25

26   **Data accessibility statement:** We (the authors) confirm that, on acceptance of the manuscript,

27   data supporting the results will be archived in Dryad data repository and a DOI will be included

28   at the end of the article.

29

30   **Key words**

31   Arctic, climate change, population dynamics, barnacle goose, trait-mediated and modified

32   effects, integral projection models, life table response experiments, transient LTRE

Abstract

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

Introduction

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

Arctic environments are seasonal and stochastic. Consequently, Arctic herbivores are exposed to variable resource availability, causing annual fluctuations in body mass and population size (Forchhammer *et al.* 2002; Couturier *et al.* 2008; Albon *et al.* 2017). Weather patterns are being modified by climate change (Scheffer *et al.* 2001), which is occurring most rapidly in the Arctic (Serreze & Barry 2011). Accordingly, climate change effects on body condition (Albon *et al.* 2017), reproduction (Post & Forchhammer 2008; Layton-Matthews *et al.* 2019a), survival (Aubry

4

70   *et al.* 2013), and population size (Forchhammer *et al.* 2002; Albon *et al.* 2017) have been

71   documented in Arctic herbivores. However, climate effects on fitness-related traits and

72   demographic rates do not act independently, and relatively little is known about the linkages

73   among them due to the challenge of quantifying these - often complex – relationships (McLean *et*

74   *al.* 2016; Visser *et al.* 2016; Jenouvrier *et al.* 2018). Additionally, traits can influence environment-

75   demography relationships via two mechanisms: trait-mediating (Ozgul *et al.* 2010; Plard *et al.*

76   2015; Albon *et al.* 2017) or trait-modifying effects (Herfindal *et al.* 2006; Harrison *et al.* 2013). A

77   mediating trait effect *explains* a relationship between environmental conditions and vital rates,

78   e.g., temperature affects body mass, which in turn affects survival, whereas a modifying effect

79   requires a body mass-temperature interaction effect on survival.

80   Since body condition is so influential on life-history processes in Arctic herbivores, we could

81   expect large population-level responses to changes in this trait (Albon *et al.* 2017). However,

82   changes in fitness-related traits do not necessarily affect population growth (McLean *et al.* 2020),

83   since three conditions must be met for trait-mediated effects on population growth to arise; (1) the

84   trait must fluctuate at the relevant life-history stage for a given, potentially age-specific,

85   demographic rate, (2) the demographic rate must be sensitive to changes in the trait, and (3) the

86   population growth rate must, in turn, be sensitive to variation in the demographic rate. If any of

87   these conditions are not met, then no pathway exists from trait variation to population growth

88   variation (Jenouvrier *et al.* 2018).

89   Populations are constantly being perturbed by short-term, temporal variation in the

90   environment (Bierzychudek 1999; Clutton–Brock & Coulson 2002). This can lead to 'transient

91   population dynamics' (Hastings 2004; Koons *et al.* 2005; Ezard *et al.* 2010), as fluctuating

92   environments cause changes in underlying population structure (e.g., age structure, Koons *et al.*

93   2016) or trait distributions (e.g., body mass, Ozgul *et al.* 2010). Changes in population structure

94   can have delayed, transient effects on future population growth, especially when there is

95   substantial variation in the vital rates of different classes of individuals (Beckerman *et al.* 2002;

96   De Roos *et al.* 2003; Hansen *et al.* 2019). If poor conditions reduce cohort body mass, vital rates

97   can be affected for several subsequent years through delayed effects, mediated by early-life body

98   mass (e.g., Albon *et al.* 1987). Recent extensions of matrix (MPM) and integral (IPM) projection

99   models have attempted to quantify population-growth consequences of such delayed ('lagged')

100 effects (Koons *et al.* 2005; Kuss *et al.* 2008). Transient life-table response experiments (transient-

101 LTREs) partition variance in the realised population growth rate into contributions from

102 demographic rates. Furthermore, they can be used to separate temporal variation in λ into direct

103 demographic effects versus delayed effects from transient changes in population structure/trait

104 distributions (e.g., cohort effects), thereby explicitly incorporating past environments

105 (Maldonado-Chaparro *et al.* 2018).

106   We explored how a substantial change in body mass contributed to variation in population

107 growth in a high-arctic herbivore, the barnacle goose (*Branta leucopsis*). We analysed female

108 mark-recapture and body mass data (1990-2017) to quantify environmental and density effects on

109 survival, reproduction, growth, and fledgling body mass. Using the regression models we

110 constructed an environmentally-driven, stochastic IPM (Rees & Ellner 2009; Metcalf *et al.* 2015).

111 Using a recently developed transient-LTRE (Maldonado-Chaparro *et al.* 2018), we decomposed

112 variation in the realised population growth rate (λ_t) into vital rate contributions through

113 demographic and trait-mediated pathways, separated into direct and delayed effects. This

114 methodology revealed that while variation in λ_t was largely reproduction-driven, through direct

115 and delayed effects (i.e., changes in age structure), body mass-mediated pathways contributed

116 negligibly to population growth. Thus, herbivore populations appear more resilient to substantial

117 changes in body condition than previously anticipated, with implications for their persistence

118 under future environmental change.

119

120 **Material and methods**

121 *Study species*

122 Arctic geese are migratory capital breeders, relying, to some extent, on accumulated body reserves

123 for reproduction (Jönsson 1997; Hahn *et al.* 2011). Therefore, an individual's body condition prior

124 to the breeding season affects their reproductive success (Ankney & MacInnes 1978; Ebbinge &

125 Spaans 1995). Svalbard barnacle geese overwinter in Scotland, UK (55° N, 3.30° W). They fly to

126 Svalbard for breeding in summer, stopping over in spring along the coast of mainland Norway.

127 The study population breeds close to Ny-Ålesund, western Spitsbergen (78°55' N, 11°56' E).

128 Geese arrive at the end of May and nest on islands in the fjord, Kongsfjorden. Hatching occurs

129 from late June. Families leave the nesting islands to forage thereafter, until offspring fledge at the

130 end of August and geese migrate back to Scotland by October.

131

132 *Demographic data*

133 All analyses were female based. Over the main study period (i.e. mark-recapture period: 1990-

134 2017), 1669 females in total were caught in July-August and ringed with unique colour and metal

135 identification bands. Recapture data were based on daily observations of ringed individuals around

136 Ny-Ålesund during the foraging period from late June to August (n_{obs} = 7280). Some years were

137 missing recapture or body mass data (see Appendix 1 for annual sample sizes). Reproduction was

138 assessed based on observations of sexually mature adults with offspring at the beginning of August

139   - when offspring fledge. Birds were divided into two age classes, individuals ringed in their first

140   year of life as 'fledglings' (*fl*) and older individuals as 'adults' (*ad*) - a pooled age class of up to

141   28 years old. Body mass was measured during a catch ($n_{measurements}$: *fl* = 696, *ad* = 2108). We

142   analysed body mass rather than other body condition proxies since body mass is a reliable measure

143   of condition in geese (Schmutz 1993; Lindholm *et al.* 1994). We tested for a temporal trend in

144   cohort body mass (1980-2017) by fitting a linear regression with year as an explanatory variable.

145

146   *Analytical approach*

147   First, we fitted (generalised) linear mixed-effects models ((G)LMMs) to describe fledgling body

148   mass (C_0), growth (i.e., change in body mass from *t* to *t+1*, *G*), overwinter survival (ϕ) and

149   reproduction: the probability of reproducing (*R*) and fledged brood size (*fec*). For each model, we

150   quantified effects of age class, body mass and covariates, using model selection. Based on the best-

151   approximating models, we constructed an IPM to model temporal dynamics of population size and

152   body mass distribution. We decomposed variation in the population growth rate (λ_t), using a

153   transient-LTRE, into direct effects of demographic rates versus indirect effects through

154   fluctuations in age class structure and body mass distribution. Contributions were further

155   decomposed into variation from modelled covariates versus random effects.

156

157   *Regression models*

158   We fitted an LMM to fledgling body mass data, to model the mean and distribution of fledgling

159   body masses (C_0), including catch date as a predictor since gosling growth exhibited a seasonal

160   trend (Appendix 2). We also fitted an LMM to body mass data of both age classes (fledglings and

161   adults), describing body mass-dependent growth between years, due to ontogeny and phenotypic

8

162   plasticity (*G*). Reproduction and mark-recapture data were modelled with GLMMs. To estimate

163   apparent survival (ϕ), mark-recapture data were modelled with a Cormack-Jolly-Seber framework

164   using the *RMark* interface (Laake 2013) for program MARK (White & Burnham 1999).

165   Reproduction was modelled as two response parameters. *R* describes the annual reproduction

166   probability i.e., whether or not a female had at least one fledgling (0/1), fitted as a binomial

167   response. Fledged brood size (*fec*) describes the number of fledglings per mother, fitted as a

168   Poisson response. Only observations from 2 year-olds onwards (the age of sexual maturity,

169   Forslund & Larsson 1992; Fjelldal *et al.* 2020) were included in the reproductive models, and the

170   model of *fec* only included successfully reproducing individuals ($R = 1$). All (G)LMM's were fitted

171   with year as a random effect in the package *lme4* (Bates *et al.* 2015).

172   We identified effects of age class, body mass, density and external covariates (see below,

173   *Covariates*) on C_0, *G, R, fec* and ϕ, using Akaike's Information Criterion corrected for small

174   sample sizes (AICc, Burnham & Anderson 2002) to identify the most parsimonious model. Body

175   mass was de-trended for model selection of *G* and C_0, to avoid spurious correlations caused by

176   declining trends. A set of candidate models were fitted for each rate including all possible subsets

177   of covariates and interactions between age class, body mass and covariates (global models shown

178   in Appendix 3, Table S1). If competing models had ΔAICc < 2, the one with least parameters was

179   considered most parsimonious. Model selection of survival rates was performed in *RMark*, but the

180   final model was fitted in a Bayesian framework to model age class-, and year-, specific random

181   effects. Markov Chain Monte Carlo (MCMC) simulations were implemented in JAGS via the *rjags*

182   package (Plummer 2013), assuming annual variation in survival originated from a random process

183   with zero mean and age class-specific deviations (see Schaub *et al.* 2013; Layton-Matthews *et al.*

184   2019b for details). All priors were non-informative. Missing body mass observations were imputed

185   by drawing from a normal distribution, where priors were set at the age class-specific mean body

186   mass and variance (Gimenez *et al.* 2006). While the Bayesian framework allows for estimation of

187   age- and year-specific random effects, sampling missing body mass data can lead to under-

188   estimation of individual heterogeneity (McCarthy & Masters 2005).

189

190   *Covariates*

191   Covariates reflecting weather and population density over the annual cycle, and predator

192   abundance effects on barnacle goose demography (Layton-Matthews *et al.* 2019a) were included

193   in the regression models of reproduction (R, *fec*), survival (ϕ), growth (G) and fledgling body mass

194   (C_0). From the overwintering grounds at Solway Firth, Scotland (*win,* i.e., winter: October$_t$ –

195   March$_{t+1}$), we included annual mean winter temperature (T_{win}) and total flyway population counts

196   (N_{win}). From the spring staging grounds at Helgeland, (*spr*, i.e., spring: April–May), we included

197   spring precipitation (P_{spr}) using data from the Vega weather station (65°38′ N, 11°52′ E). Climate

198   covariates from the breeding grounds in Svalbard (*sum,* i.e., summer) included the date of spring

199   onset (SO_{sum}), i.e., the ordinal day when the 10-day smoothed daily temperature crossed 0°C and

200   remained above for at least 10 days (Le Moullec *et al.* 2019), temperature (mid-June–mid-July,

201   T_{sum}) and precipitation (mid-July–mid-August, P_{sum}). Estimated adult population size in

202   Kongsfjorden (N_{sum}, Layton-Matthews *et al.* 2019b) was also included, and also the proportion of

203   occupied known dens as an index of Arctic fox (*Vulpes lagopus*) abundance (*fox$_{sum}$*), since

204   predation by Arctic foxes affects pre-fledging survival (Fuglei *et al.* 2003; Layton-Matthews *et al.*

205   2019a). More details on covariates can be found in Layton-Matthews *et al.* (2019a).

206

207   *Stochastic integral projection model*

208 We constructed a stochastic IPM, describing temporal dynamics of population size and body mass

209 distribution, $n(z, t)$, of fledglings (*fl*) and adults (*ad*), following the life cycle in Fig. 1. The growth

210 kernel, $G^{(t)}(z', z)$, describes the probability density function of body masses z' in August in year

211 $t+1$ of an individual of body mass z in year t. Annual age-class specific survival, $\phi^{(t)}(z, a)$, describes

212 the probability of an individual, of age class a (*fl* or *ad*) and body mass z at year t, surviving to

213 year $t+1$. $P_{ad}^{(t)}(z', z)$ and $P_{fl}^{(t)}(z', z)$ represent survival-growth kernels for adults and fledglings

214 describing how individuals of body mass z at time t, survive and grow to reach mass z' at $t+1$,

215 given by:

216 $P_a^{(t)}(z', z) = \phi^{(t)}(z, a)\, G^{(t)}(z', z)$ for $a = $ *fledgling* or *adults*   (1)

217   Annual reproduction probability, $R^{(t)}(z)$, describes the probability of a >1-year-old female

218 of body mass z producing at least one fledgling at $t+1$, given she survives. Fledged brood size,

219 $fec^{(t)}$, describes the number of fledglings per mother at $t+1$, conditional on reproduction. Fledgling

220 body mass kernel, $C_0^{(t)}(z')$, describes the probability distribution of fledgling body masses in

221 August at $t+1$. This was assumed to be independent of mother body mass, since a pedigree was not

222 available, which is likely a fair assumption since offspring body mass has not been linked to mother

223 body mass, rather to structural size (e.g., head size, Larsson *et al.* 1998). $F_{ad}^{(t)}(z', z)$ is the

224 reproduction kernel, describing the density of fledglings of body mass z' that adults of body mass

225 z can contribute to the population at year $t+1$;

226 $F_{ad}(z', z) = \phi^{(t)}(z, ad)\, R^{(t)}(z)\, fec^{(t)}\, C_0^{(t)}(z')\, /2$ (2)

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

228 $n_{fl}(z', t+1) = \int_L^U F_{ad}^{(t)}(z', z)\, n_{ad}(z, t)\, dz$ (3)

229 $n_{ad}(z', t+1) = \int_L^U P_{ad}^{(t)}(z', z)\, n_{ad}(z, t)\, dz + \int_L^U P_{fl}^{(t)}(z', z)\, n_{fl}(z, t)\, dz$ (4)

230   We numerically integrated the IPM using the 'midpoint rule' (Easterling *et al.* 2000) with

231   lower (L) and upper (U) integration limits of body mass 400 and 2500 grams, to avoid eviction of

232   individuals from the model. The IPM assumed density-independent population growth, since

233   density effects on survival exhibited a linear temporal trend that would have imposed extreme

234   restrictions on the model. Stochastic population dynamics were simulated over 100,000 years

235   using a two-step MCMC resampling approach (Metcalf *et al.* 2015). For each year, a set of

236   environment/density covariate values was sampled from 28 observations in this study (1990–2017).

237   For each function (C_0, G, R, *fec*, ϕ_{fl} and ϕ_{ad}) values were sampled from their respective distributions

238   (i.e., distribution sampling, Metcalf *et al.* 2015). We used estimates of intercept and yearly random

239   effects to calculate a variance-covariance matrix and sampled parameter sets assuming a

240   multivariate normal distribution (Gelman & Hill 2006), to account for potential correlations

241   (Compagnoni *et al.* 2016). Trends in demographic rates, growth or fledgling body mass were

242   captured as random effects but were not explicitly included in the simulation, since temporal

243   variation was assumed to be independent and identically distributed (i.i.d.) over time. Transition

244   kernels for each annual projection were constructed by combining both sets of sampled parameters

245   to calculate realised intercepts and slopes for each function.

246

Transient life table response experiment

248   We used an extension of the Monte Carlo random LTRE, introduced by Rees and Ellner (2009),

249   to incorporate transient fluctuations in age class-structure and body mass distribution

250   (Maldonado-Chaparro *et al.* 2018). Rather than assuming the population was always close to its

251   stable structure, i.e., focusing on the yearly asymptotic growth rates ($\tilde{\lambda}_t$), we decomposed variance

252   in the realised population growth rate at time *t* (λ_t). We included lagged parameter effects in the

253   model of λ_t, to quantify delayed effects of parameters (i.e., parameter i at time t, $\theta_{i,t}$), acting through

254   changes in age structure or body mass distribution. Variance decompositions of λ_t were modelled

255   assuming either linear (linear model, LM) or non-linear (generalised additive model, GAM)

256   dependencies of λ_t. Following Maldonado-Chaparro *et al.* (2018), we decomposed variance in log(

257   λ_t). We compared the R^2 of LMs and GAMs and incorporated delayed effects with increasing

258   numbers of year lags. We also tested whether interaction effects between parameters (pairwise

259   smooths for GAMs) contributed to substantial variation in log(λ_t). We considered a model of log(

260   λ_t) to be a better fit when the amount of variance explained increased by at least 1%

261   (Maldonado-Chaparro *et al.* 2018).

262   Vital rate contributions were further partitioned into variation from modelled covariates

263   effects versus random effects. In this case, (net) contributions of covariates to λ_t depended on; (1)

264   temporal covariances among covariates, (2) their effect size on $\theta_{i,t}$ and (3) the sensitivity of λ_t to

265    $\theta_{i,t}$. We assumed linear dependencies of λ_t on $\theta_{i,t}$ for the environmental decomposition. In the IPM,

266   trait-mediated effects could contribute to intercept variation in each function (e.g., G or ϕ), while

267   trait-modified effects would cause variation in the slope describing the relationship between body

268   mass and a function. Consequently, we decomposed variation in log(λ_t) at three hierarchical levels:

269   (1) overall contributions from C_0, G, R, *fec* and ϕ, (2) modelled environment versus random effects

270   and (3) slope versus intercept variation.

271

272   **Results**

273   *Body mass and life history processes*

274   The best-approximating model of overwinter survival (ϕ) included an interaction effect between

275   age class and body mass, with a much stronger positive effect on fledglings (Fig. 1a), and additive

13

276 effects of overwintering population size (N_{win}, negative effect) and winter temperature (T_{win},

277 positive effect) (Table 1). The best growth model (G), estimating body mass at year t+1, included

278 a positive effect of body mass at t (Fig. 1b). The best model of reproduction probability (i.e., of an

279 adult female producing fledglings, R) included spring precipitation (positive effect, P_{spr}) and date

280 of spring onset (negative effect, SO_{sum}), and an interaction effect between mother body mass and

281 SO_{sum}, with a strong, positive body mass effect in late springs and no effect in early springs (Fig.

282 1c-e). For fledged brood size (*fec*), the best model included negative effects of Arctic fox

283 abundance (fox_{sum}) and summer precipitation (P_{sum}). The best model of fledgling body mass (C_0)

284 included an interaction effect of fox_{sum} and adult population density at the breeding grounds (N_{sum}),

285 where N_{sum} tended to have a negative effect only at high fox abundance (Fig. 1f-h). Further

286 description of the model selection and associated tables (Tables S2.1-2.5) can be found in

287 Appendix 3.

288 Over the study period, average cohort body mass declined significantly (slope = -8.3 g per

289 cohort, SE = 0.8 g, p<0.001). Inter-annual changes in body mass were relatively small for adults,

290 but larger for fledglings (Fig. 2).

291

292 *Transient LTRE*

293 The mean stochastic population growth rate $\hat{\lambda}_t$ was 1.07 (confidence interval: 0.77, 1.59)

294 (Appendix S4, Fig. S1), which was similar to the observed growth rate (1.05; 0.65, 1.53). The

295 stable body mass-age class distribution reflected the bimodal distribution of fledgling and adult

296 body mass (Appendix S4, Fig. S2). 94% of the variation in λ_t was explained by main effects of the

297 functions, including a one-year time lag, with the transient linear LTRE (LM-LTRE), which

298 increased to 98% with a generalised additive model (GAM-LTRE). The only pairwise smooth

299   (interaction between parameters) explaining more than 1% variance was between the intercept and

300   slope terms of reproduction probability (R) - since SO_{sum} was a predictor in both terms. Parameter

301   effects with more than a one-year lag explained <1% of the variance in λ_t.

302   Sensitivity surfaces were estimated using the GAM-LTRE for $\log(\lambda_t)$, illustrating the

303   influence of each function through direct (Fig. 3a) and delayed effects (Fig. 3b). Direct effects of

304   variation operating through reproduction probability (R) was larger than survival (ϕ) or fledged

305   brood size (*fec*). λ_t was sensitive to variation through survival rates, especially adult survival (Fig.

306   3a). Note that direct effects of variation through changes in growth and fledgling body mass are

307   not included in Fig. 3a since changes in body mass only affect λ the following year (i.e., delayed

308   effects). The population growth rate was insensitive to delayed effects (Fig. 3b) through G and C_0

309   (i.e., trait-mediated effects). The sensitivity of λ_t to delayed effects (i.e., at t-1) through R and *fec*

310   reflects how increased reproduction in a given year had a negative impact the following year, via

311   a shift in the age structure towards a larger proportion of non-reproductive individuals.

312   Vital rate contributions from variances and covariances in $\log(\lambda_t)$, separating variance

313   explained by covariates versus random effects, indicated large contribution from variation in the

314   reproductive probability (R) (Fig. 4). R contributed 69% through direct effects and 12% through

315   delayed effects (i.e., changes in age structure). The remaining ~20% was largely explained by

316   direct and delayed contributions from variation in adult survival (ϕ_{ad}, total contribution = 6%),

317   fledged brood size (*fec*, 6%), and fledgling survival (ϕ_{fl}, 2%). Changes in body mass acting through

318   fledgling body mass and growth functions (i.e., trait-mediated effects) made negligible

319   contributions to variance in λ (0.04% through G and 0.5% through C_0). Reproduction (R, *fec*) was

320   negatively correlated with adult survival (ϕ_{ad}), resulting in a total contribution of -7% to $\log(\lambda_t)$,

321   i.e., high adult survival in one year meant lower reproduction, thereby reducing temporal variation

322   in λ. Both reproductive parameters (R and *fec*) and survival parameters (ϕ_{fl} and ϕ_{ad}) positively

323   covaried, and both covariations contributed ca. 3% to $\log(\lambda_t)$.

324   58% of the variation in $\log(\lambda_t)$ acting through reproduction probability (R) was attributed

325   to modelled covariates (Fig. 4). Precipitation at the spring stopover site (P_{spr}) contributed to 26%

326   of the variation, while date of spring onset at the breeding grounds (SO_{sum}) contributed 16%

327   through intercept and slope variance. 59% of the variation in $\log(\lambda_t)$ that was attributed to adult

328   survival (ϕ_{ad}) was explained by temperature (T_{win}) and population size (N_{win}) at the wintering

329   grounds, accounting for 1% and 2% of the overall variation in $\log(\lambda_t)$. In contrast, < 1% of the

330   variation in fledgling survival was attributed to T_{win} and N_{win} although these covariates explained

331   95% of the positive covariation between fledgling and adult survival, leading to a positive

332   contribution of ca. 1% to variation in $\log(\lambda_t)$ (Fig. 4). Finally, 65% of the variation in $\log(\lambda_t)$

333   through fledged brood size (*fec*) was explained by Arctic fox abundance and summer precipitation,

334   each contributing 3% to variation in $\log(\lambda_t)$.

335

Discussion

337   Coupled trait-demography responses to environmental change may be key to understand and

338   predict short- and long-term population dynamics, especially in Arctic herbivores. Here, we have

339   explored population growth responses to a substantial decline in body mass in an Arctic goose

340   population, using a recently developed transient-LTRE. Body mass at fledging was density-

341   dependent (Fig. 1f-h), supporting previous findings that the temporal decline in body mass – a

342   phenomenon observed across Arctic goose species (Cooch *et al.* 1991b; Larsson *et al.* 1998) – was

343   caused by habitat degradation at the breeding grounds. However, population growth appeared

344   buffered against these changes in body mass (Fig. 3b, Table 2), despite the strong influence of this

345   body condition proxy on reproduction and survival (Fig. 1a, c-e). Instead, variation in population

346   growth rates was largely explained by direct and delayed effects operating through reproduction,

347   partly caused by annual variation in spring phenology at the breeding grounds (Fig. 4).

348   Both resident and migrant Arctic herbivores are exposed to highly variable weather conditions,

349   which can lead to variation in body condition and population size (Festa-Bianchet *et al.* 1997;

350   Sæther 1997). Although effects of population density and weather on body mass are well

351   documented in herbivores, whether these effects extend to variation in population growth remains

352   largely unanswered. Goose populations have expanded across the Arctic, as a result of increasing

353   numbers caused by hunting bans and agricultural change at overwintering grounds (Madsen &

354   Cracknell 1999; Fox & Madsen 2017). Density-dependent processes associated with overgrazing

355   by geese have degraded the Arctic breeding grounds, leading to declining cohort body size and

356   mass of Arctic geese (Cooch *et al.* 1991b; Loonen *et al.* 1997; Reed & Plante 1997; Larsson *et al.*

357   1998). Average cohort body mass of the study population has declined by 10% from 1980–2017.

358   We documented density dependence in fledgling body mass, although this was only evident at

359   high Arctic fox abundance, i.e. the main predator of the goslings and, occasionally, adults (Fuglei

360   *et al.* 2003). Foxes therefore influenced geese both through lethal effects on fledged brood size

361   (*fec*) and non-lethal effects on fledgling body mass, by inducing density-dependent restrictions on

362   their ability to utilise all available foraging areas (Loonen *et al.* 1998).

363   Despite the temporal decline in (cohort) body mass, between-year fluctuations in adult body

364   mass were rather small. Fledgling body mass exhibited more inter-annual variation, likely a result

365   of strong resource dependence during gosling growth (Cooch *et al.* 1991a; Lindholm *et al.* 1994).

366   Body mass, in turn, positively influenced survival and reproduction. The reserves first-year-geese

367   accumulate at the breeding grounds affect survival during migration (Owen & Black 1989; Menu

368 *et al.* 2005), reflected in the strong positive effect of body mass on fledgling overwinter survival

369 found here. Adult survival, however, was largely unaffected by body mass and varied less inter-

370 annually.

371 Several studies have stressed the potential importance of coupled trait-demography responses

372 in predicting population persistence under environmental change (Ozgul *et al.* 2009; 2010; Plard

373 *et al.* 2014; Jenouvrier *et al.* 2018). However, some studies have indicated that changes in traits

374 may lead to more limited population-level responses than expected (Wilson & Arcese 2003;

375 Maldonado-Chaparro *et al.* 2018; McLean *et al.* 2020). Here, despite the potential for coupled

376 body mass-demography responses, changes in the body mass of Arctic geese did not incur

377 population-level responses through trait-mediated effects. Over the study period, body mass

378 underwent a temporal decline and positively influenced demographic rates. However, fluctuations

379 in body mass did not translate into effects on population growth because all three conditions

380 required for trait-mediated pathways to arise were not met for any age class-specific demographic

381 rate (Table 2). Although fledging survival (ϕ_{fl}) was influenced by body mass, variance in ϕ_{fl} only

382 made a negligible contribution to λ since fledglings represent only a small fraction of the

383 population. In contrast, population growth was sensitive to changes in adult survival, but body

384 mass had close to no effect on adult survival (ϕ_{ad}). Variation in λ through ϕ_{ad} was attributed to

385 overwinter temperature and population density. Population growth was highly sensitive to changes

386 in reproduction probability, which was only weakly influenced by adult body mass (at mean

387 environmental conditions), showing a pronounced long-term decline yet limited inter-annual

388 variation. This resulted in a lack of trait-mediated effects through reproduction (*R*). Nevertheless,

389 further changes in body mass could have large effects on λ, operating through *R*. According to the

390 demographic buffering hypothesis, variability in λ reduces fitness (Tuljapurkar 1982), leading to

18

391 selection for reduced variation (Gaillard & Yoccoz 2003; Jongejans *et al.* 2010). Therefore,

392 buffering of population growth against trait-mediated variation may have occurred via such

393 mechanisms.

394   Quantifying demographic - and associated trait - responses to climate change is necessary for

395 a mechanistic and predictive understanding of population-level consequences (Jenouvrier 2013;

396 Paniw *et al.* 2019a). Arctic warming is advancing snow melt, with widespread effects on plant

397 phenology, while rising summer temperatures are influencing plant productivity (Bjorkman *et al.*

398 2020). For migrating Arctic geese, spring phenology at the breeding grounds also dictates when

399 nesting sites become snow-free as well as the onset of plant growth: both important determinants

400 of breeding success (Reed *et al.* 2004; Madsen *et al.* 2007). The positive effect of earlier spring

401 onset on fledgling production in our study population has previously been attributed to females

402 laying bigger clutches with improved hatching success (Layton-Matthews *et al.* 2019a).

403 Advancing spring phenology could therefore benefit reproduction and population growth, which

404 appears unhampered by the temporal decline in body mass (i.e., since effects of body mass on

405 reproduction diminish with earlier springs). However, neither *R* nor *fec* exhibited positive temporal

406 trends (Appendix 5) likely due to contrasting direct versus indirect climate change effects, as the

407 number of Arctic foxes – and thus gosling predation rates – are generally increasing (Layton-

408 Matthews *et al.* 2019a; unpublished data, E. Fuglei).

409   In capital breeders, such as Arctic geese, accumulating body stores is beneficial in

410 unpredictable environments, and this strategy is therefore typical at higher latitudes (Varpe *et al.*

411 2009; Sainmont *et al.* 2014). Storing resources along their flyway allows geese to initiate

412 reproduction without immediate food access (Klaassen *et al.* 2017). Consequently, several

413 reproductive stages are dependent on fat reserves (Bêty *et al.* 2003; Guillemain *et al.* 2008; Aubry

414 *et al.* 2013), reflected here in the positive relationship between body mass and reproduction

415 probability. Heavier individuals were more likely to reproduce than lighter ones under poor

416 (delayed) spring conditions, since they have more 'capital' to initiate reproduction (i.e., a trait-

417 modified climate effect). However, in earlier springs (i.e. typically in more recent years), possibly

418 with excess nesting sites and food resources, benefits of accumulating fat reserves were reduced

419 and the influence of body mass on reproduction was weaker. Further advanced springs due to

420 continued climate change could therefore tip the balance in favour of accumulating fewer resources

421 for reproduction, potentially relaxing selection on body mass if individuals gain a survival

422 advantage by requiring fewer fat reserves for migration (Larsson *et al.* 1998).

423 Overall, population dynamics of Arctic migratory geese appear largely unaffected by the

424 decline in body mass, thus far. Buffering population growth against changes in body condition –

425 which is essential for survival and reproduction in Arctic herbivores - has clear implications for

426 their resilience to future environmental change. However, as the Arctic continues to change,

427 further body mass declines could potentially have big effects on population growth, in this case

428 via trait-mediated effects through reproduction.

429 This work emphasises the importance of holistic approaches fully capturing pathways from

430 environmental variation to individual and population-level responses. Even when environmental

431 change substantially alters trait distributions that are correlated with vital rates, we cannot assume

432 this will have consequences for population persistence.

433

440   **Tables**

441   **Table 1.** Linear predictors for best-approximating regression models of each function, with mean

442   parameter estimates, used to parameterise the integral projection model (IPM). Functions included

443   the covariates; winter temperature (T_{win}) and overwinter population size (N_{win}) in Scotland, Arctic

444   fox abundance (fox_{sum}), adult population size (N_{sum}), the date of spring onset (SO_{sum}) and summer

445   precipitation (P_{sum}) at the breeding grounds on Svalbard, and spring precipitation at the spring

446   stopover site at Helgeland (P_{spr}). a is a dummy variable equal to 0 for fledglings (fl) and 1 for

447   adults (ad), and z refers to body mass and ***catch*** refers to catch date.

448

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

449 **Table 2.** Summary of which conditions for body mass-mediated effects on the population growth

450 rate (for each demographic rate) that were met or not (✓ = condition met).

| Condition	Fledgling survival (ϕ_{fl})	Adult survival (ϕ_{ad})	Reproduction probability (R)	Fledged brood size (*fec*)
Body mass fluctuates at the relevant stage	✓			
Demographic rate sensitive to body mass change	✓		✓	
λ sensitive to variation in demographic rate		✓	✓	✓

451

452

23

453   **Figures**
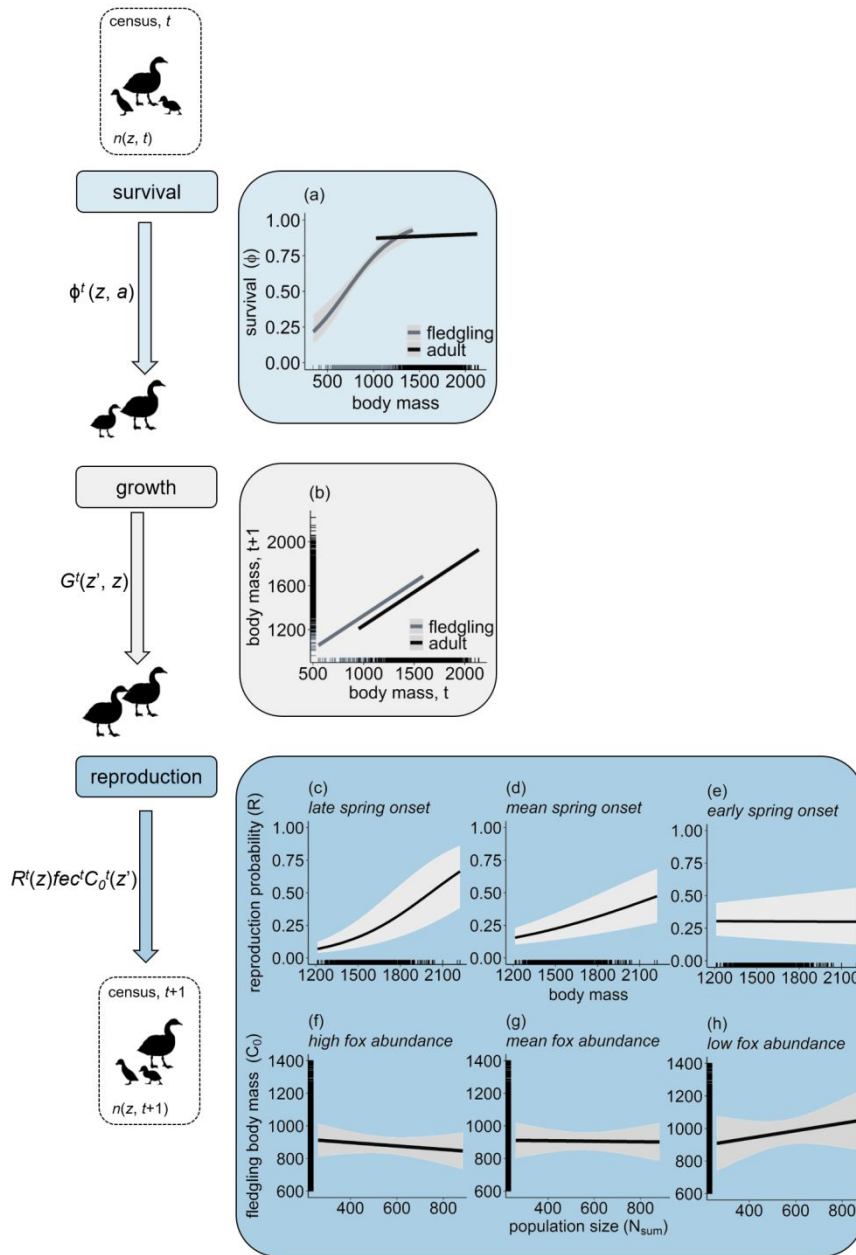
454   **Figure 1.** Life cycle of barnacle geese based on a post-breeding census (i.e., breeding occurs just

455   before a census). Individuals in age class *a* must survive with a body mass-dependent probability

456   ($\phi(z, a)$) and grow to the next year ($G(z', z)$) in order to reproduce ($R(z)$, *fec*) and contribute

457   fledglings of body mass ($C_0(z')$) to the population. Model predictions of body mass effects at *t* on;

458   (a) fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, (b) body mass at *t*+1, reproduction probability (R) of

459   adult females at the (c) 20th quantile, (d) mean and (e) 80th quantile of the date of spring onset

460   (SO_{sum}). Effects of adult population size at Ny-Ålesund (N_{sum}) on fledgling body mass (C_0) at the

461   (f) 20th, (g) mean and (h) 80th quantile of Arctic fox abundance (fox_{sum}).
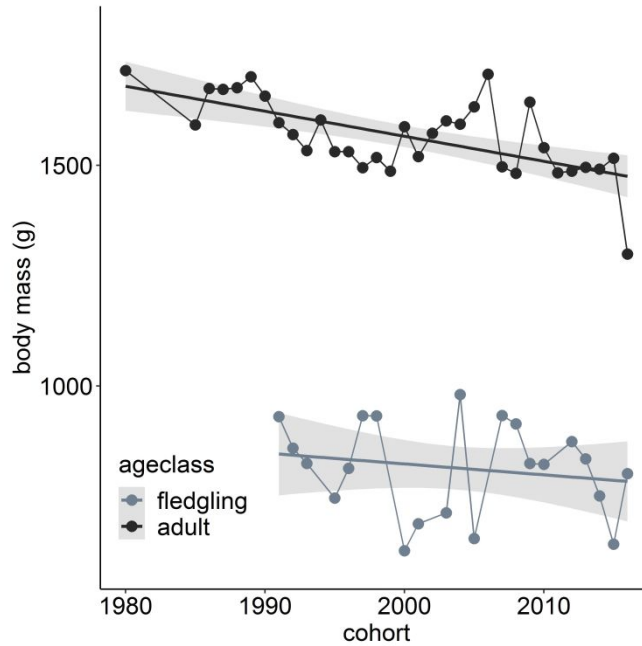
Figure 2. Temporal trends in average cohort adult (black, 1980-2016) and annual fledgling

(grey, 1991-2016) body mass. Slope (bold line) with 95% confidence intervals (shading) were

calculated based on a linear regression.
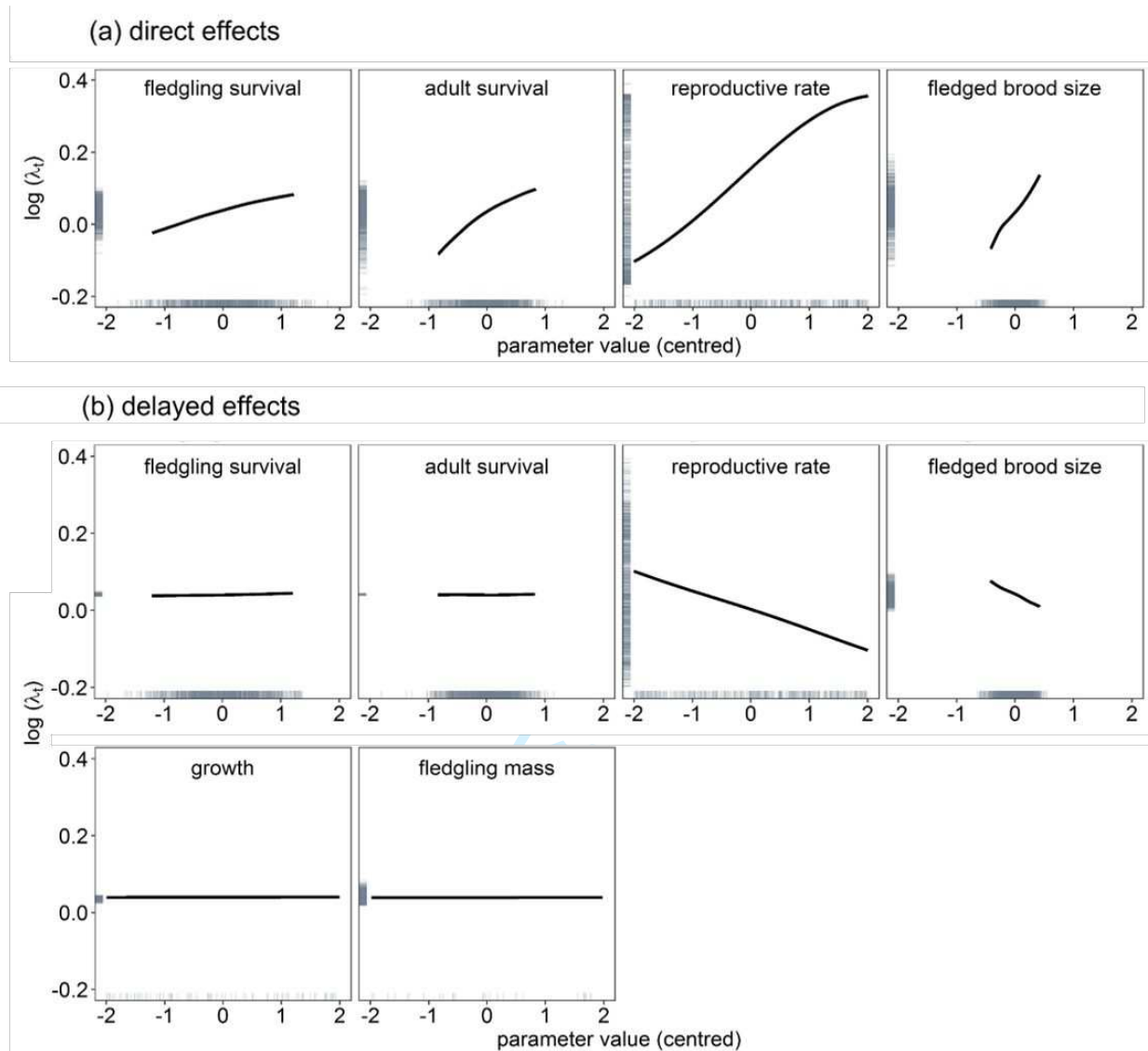
Figure 3. Sensitivity surfaces illustrating the effects of fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, reproductive rate (R), fledged brood size (*fec*), growth (*G*), and fledgling body mass (C_0) on the population growth rate, $\log(\lambda_t)$. Contributions from each vital rate parameter were separated into (a) direct and (b) delayed contributions, i.e., parameter effects at *t* and *t*-1, respectively, on $\log(\lambda_t)$. The x-axis and y-axis rugs show distributions of parameters (centred values) and $\log(\lambda_t)$, respectively.
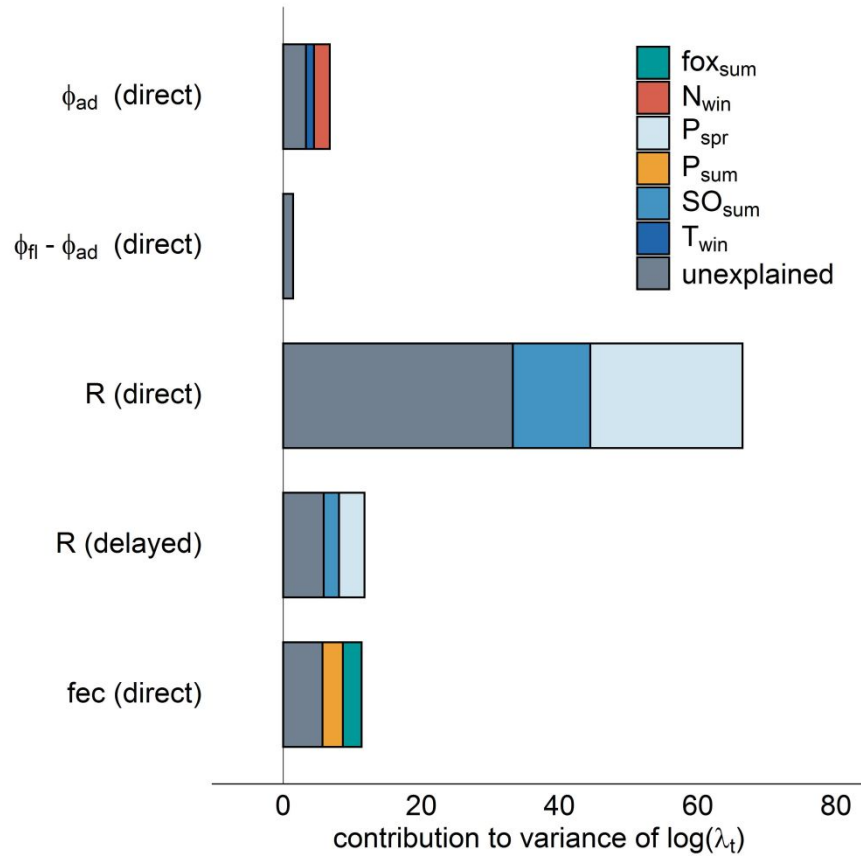
Figure 4. Percentage contributions of the largest demographic contributions (through adult survival, ϕ_{ad}, fledgling survival, ϕ_{fl}, reproduction probability, R and fledged brood size, *fec*) to variance in the population growth rate, $\log(\lambda_t)$. Contributions were decomposed into direct and delayed variances and covariances. Colours represent contributions from modelled covariates versus unexplained variation (random effects).

477 **References**

478 Albon, S., Clutton-Brock, T. & Guinness, F. (1987). Early development and population

479   dynamics in red deer. II. Density-independent effects and cohort variation. *The Journal of*

480   *Animal Ecology*, 69-81.

481 Albon, S.D., Irvine, R.J., Halvorsen, O., Langvatn, R., Loe, L.E., Ropstad, E. *et al.* (2017).

482   Contrasting effects of summer and winter warming on body mass explain population

483   dynamics in a food-limited Arctic herbivore. *Global Change Biology*, 23, 1374-1389.

484 Ankney, C.D. & MacInnes, C.D. (1978). Nutrient reserves and reproductive performance of

485   female Lesser Snow Geese. *The Auk*, 459-471.

486 Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P. & Koons, D.N. (2013).

487   Climate change, phenology, and habitat degradation: drivers of gosling body condition

488   and juvenile survival in lesser snow geese. *Global Change Biology*, 19, 149-160.

489 Bates, D., Machler, M., Bolker, B.M. & Walker, S.C. (2015). Fitting Linear Mixed-Effects

490   Models Using lme4. *Journal of Statistical Software*, 67, 1-48.

491 Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V. & Lundberg, P. (2002). Population dynamic

492   consequences of delayed life-history effects. *Trends in Ecology & Evolution*, 17, 263-

493   269.

494 Bêty, J., Gauthier, G. & Giroux, J.-F. (2003). Body condition, migration, and timing of

495   reproduction in snow geese: a test of the condition-dependent model of optimal clutch

496   size. *The American Naturalist*, 162, 110-121.

497 Bierzychudek, P. (1999). Looking backwards: assessing the projections of a transition matrix

498   model. *Ecological Applications*, 9, 1278-1287.

499   Bjorkman, A.D., García Criado, M., Myers-Smith, I.H., Ravolainen, V., Jónsdóttir, I.S.,

500   Westergaard, K.B. *et al.* (2020). Status and trends in Arctic vegetation: Evidence from

501   experimental warming and long-term monitoring. *Ambio*, 49, 678-692.

502   Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A*

503   *Practical Information-Theoretic Approach*. 2nd edn. Springer Science & Business Media,

504   New York, USA.

505   Choudhury, S., Black, J.M. & Owen, M. (1996). Body size, fitness and compatibility in barnacle

506   geese Branta leucopsis. *Ibis*, 138, 700-709.

507   Clutton–Brock, T. & Coulson, T. (2002). Comparative ungulate dynamics: the devil is in the

508   detail. *Philosophical Transactions of the Royal Society of London. Series B: Biological*

509   *Sciences*, 357, 1285-1298.

510   Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneck, M.E. *et al.*

511   (2016). The effect of demographic correlations on the stochastic population dynamics of

512   perennial plants. *Ecological Monographs*, 86, 480-494.

513   Cooch, E., Lank, D., Dzubin, A., Rockwell, R. & Cooke, F. (1991a). Body size variation in

514   lesser snow geese: environmental plasticity in gosling growth rates. *Ecology*, 72, 503-

515   512.

516   Cooch, E., Lank, D., Rockwell, R. & Cooke, F. (1991b). Long-term decline in body size in a

517   snow goose population: evidence of environmental degradation? *The Journal of Animal*

518   *Ecology*, 483-496.

519   Couturier, S., Cote, S.D., Huot, J. & Otto, R.D. (2008). Body-condition dynamics in a northern

520   ungulate gaining fat in winter. *Canadian Journal of Zoology*, 87, 367-378.

521   De Roos, A.M., Persson, L. & McCauley, E. (2003). The influence of size-dependent life-history

522   traits on the structure and dynamics of populations and communities. *Ecology Letters*, 6,

523   473-487.

524   Douhard, M., Gaillard, J.-M., Delorme, D., Capron, G., Duncan, P., Klein, F. *et al.* (2013).

525   Variation in adult body mass of roe deer: early environmental conditions influence early

526   and late body growth of females. *Ecology*, 94, 1805-1814.

527   Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000). Size-specific sensitivity: applying a new

528   structured population model. *Ecology*, 81, 694-708.

529   Ebbinge, B.S. & Spaans, B. (1995). The importance of body reserves accumulated in spring

530   staging areas in the temperate zone for breeding in dark-bellied brent geese Branta b.

531   bernicla in the high Arctic. *Journal of Avian Biology*, 105-113.

532   Ezard, T.H., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A. *et al.* (2010).

533   Matrix models for a changeable world: the importance of transient dynamics in

534   population management. *Journal of Applied Ecology*, 47, 515-523.

535   Festa-Bianchet, M., Jorgenson, J.T., Bérubé, C.H., Portier, C. & Wishart, W.D. (1997). Body

536   mass and survival of bighorn sheep. *Canadian Journal of Zoology*, 75, 1372-1379.

537   Fjelldal, M.A., Layton-Matthews, K., Lee, A.M., Grøtan, V., Loonen, M.J. & Hansen, B.B.

538   (2020). High-Arctic family planning: earlier spring onset advances age at first

539   reproduction in barnacle geese. *Biology Letters*, 16, 20200075.

540   Forchhammer, M.C., Post, E., Stenseth, N.C. & Boertmann, D.M. (2002). Long-term responses

541   in arctic ungulate dynamics to changes in climatic and trophic processes. *Population*

542   *Ecology*, 44, 113-120.

543   Forslund, P. & Larsson, K. (1992). Age-related reproductive success in the barnacle goose.

544   *Journal of Animal Ecology*, 61, 195-204.

545   Fox, A.D. & Madsen, J. (2017). Threatened species to super-abundance: The unexpected

546   international implications of successful goose conservation. *Ambio*, 46, 179-187.

547   Fuglei, E., Øritsland, N.A. & Prestrud, P. (2003). Local variation in arctic fox abundance on

548   Svalbard, Norway. *Polar Biology*, 26, 93-98.

549   Gaillard, J.-M. & Yoccoz, N.G. (2003). Temporal variation in survival of mammals: a case of

550   environmental canalization? *Ecology*, 84, 3294-3306.

551   Gelman, A. & Hill, J. (2006). Causal inference using multilevel models. In: *Data analysis using*

552   *regression and multilevel/hierarchical models*. Cambridge University Press Cambridge,

553   UK, pp. 503-512.

554   Gimenez, O., Covas, R., Brown, C.R., Anderson, M.D., Brown, M.B. & Lenormand, T. (2006).

555   Nonparametric estimation of natural selection on a quantitative trait using mark-recapture

556   data. *Evolution*, 60, 460-466.

557   Guillemain, M., Elmberg, J., Arzel, C., Johnson, A.R. & Simon, G. (2008). The income–capital

558   breeding dichotomy revisited: late winter body condition is related to breeding success in

559   an income breeder. *Ibis*, 150, 172-176.

560   Hahn, S., Loonen, M.J.J.E. & Klaassen, M. (2011). The reliance on distant resources for egg

561   formation in high Arctic breeding barnacle geese Branta leucopsis. *Journal of Avian*

562   *Biology*, 42, 159-168.

563   Hansen, B.B., Gamelon, M., Albon, S.D., Lee, A.M., Stien, A., Irvine, R.J. *et al.* (2019). More

564   frequent extreme climate events stabilize reindeer population dynamics. *Nature*

565   *communications*, 10, 1616.

566 Harrison, X.A., Hodgson, D.J., Inger, R., Colhoun, K., Gudmundsson, G.A., McElwaine, G. *et*

567   *al.* (2013). Environmental conditions during breeding modify the strength of mass-

568   dependent carry-over effects in a migratory bird. *PloS one*, 8, e77783.

569 Hastings, A. (2004). Transients: the key to long-term ecological understanding? *Trends in*

570   *Ecology & Evolution*, 19, 39-45.

571 Herfindal, I., Sæther, B.E., Solberg, E.J., Andersen, R. & Høgda, K.A. (2006). Population

572   characteristics predict responses in moose body mass to temporal variation in the

573   environment. *Journal of Animal Ecology*, 75, 1110-1118.

574 Jenouvrier, S. (2013). Impacts of climate change on avian populations. *Global Change Biology*,

575   19, 2036-2057.

576 Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K. *et al.* (2018).

577   Climate change and functional traits affect population dynamics of a long-lived seabird.

578   *Journal of Animal Ecology*, 87, 906-920.

579 Jongejans, E., De Kroon, H., Tuljapurkar, S. & Shea, K. (2010). Plant populations track rather

580   than buffer climate fluctuations. *Ecology Letters*, 13, 736-743.

581 Jönsson, K.I. (1997). Capital and income breeding as alternative tactics of resource use in

582   reproduction. *Oikos*, 78, 57-66.

583 Klaassen, M., Hahn, S., Korthals, H. & Madsen, J. (2017). Eggs brought in from afar:

584   Svalbard-breeding pink-footed geese can fly their eggs across the Barents Sea. *Journal of*

585   *Avian Biology*, 48, 173-179.

586 Koons, D.N., Grand, J.B., Zinner, B. & Rockwell, R.F. (2005). Transient population dynamics:

587   relations to life history and initial population state. *Ecological modelling*, 185, 283-297.

588   Koons, D.N., Iles, D.T., Schaub, M. & Caswell, H. (2016). A life-history perspective on the

589   demographic drivers of structured population dynamics in changing environments.

590   *Ecology letters*, 19, 1023-1031.

591   Kuss, P., Rees, M., Ægisdóttir, H.H., Ellner, S.P. & Stöcklin, J. (2008). Evolutionary

592   demography of long-lived monocarpic perennials: a time-lagged integral projection

593   model. *Journal of Ecology*, 96, 821-832.

594   Laake, J.L. (2013). RMark: an R interface for analysis of capture-recapture data with MARK. In:

595   *AFSC Processed Report 2013-01*. Alaska Fisheries Science Center, National Marine

596   Fisheries Service, NOAA Seattle, Washington, USA.

597   Labocha, M.K. & Hayes, J.P. (2012). Morphometric indices of body condition in birds: a review.

598   *Journal of Ornithology*, 153, 1-22.

599   Lande, R., Engen, S. & Saether, B.-E. (2003). *Stochastic population dynamics in ecology and*

600   *conservation*. Oxford University Press, Oxford, UK.

601   Larsson, K., Van der Jeugd, H.P., Van der Veen, I.T. & Forslund, P. (1998). Body size declines

602   despite positive directional selection on heritable size traits in a barnacle goose

603   population. *Evolution*, 52, 1169-1184.

604   Layton-Matthews, K., Hansen, B.B., Grøtan, V., Fuglei, E. & Loonen, M.J.J.E. (2019a).

605   Contrasting consequences of climate change for migratory geese: predation, density

606   dependence and carryover effects offset benefits of high-arctic warming. *Global Change*

607   *Biology*, 26, 642-657.

608   Layton-Matthews, K., Loonen, M.J.J.E., Hansen, B.B., Saether, B.-E., Coste, C.F.D. & Grøtan,

609   V. (2019b). Density-dependent population dynamics of a high Arctic capital breeder, the

610   barnacle goose *Journal of Animal Ecology*, 88, 1191-1201.

611 Le Moullec, M., Buchwal, A., van der Wal, R., Sandal, L. & Hansen, B.B. (2019). Annual ring

612   growth of a widespread high arctic shrub reflects past fluctuations in community-level

613   plant biomass. *Journal of Ecology*, 107, 436-451.

614 Lindholm, A., Gauthier, G. & Desrochers, A. (1994). Effects of hatch date and food supply on

615   gosling growth in arctic-nesting Greater Snow Geese. *Condor*, 96, 898-908.

616 Loonen, M.J.J.E., Oosterbeek, K. & Drent, R. (1997). Variation in growth of young and adult

617   size in barnacle geese Branta leucopsis: evidence for density dependence. *Ardea*, 85, 177-

618   192.

619 Loonen, M.J.J.E., Tombre, I.M. & Mehlum, F. (1998). Development of an arctic barnacle goose

620   colony: interactions between density and predation. *Norsk Polarinstitutt Skrifter*, 200, 67-

621   80.

622 Madsen, J. & Cracknell, G. (1999). *Goose populations of the Western Palearctic: a review of*

623   *status and distribution*. National Environmental Research Institute, Denmark and

624   Wetlands International, Wageningen, The Netherlands.

625 Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F. *et al.* (2007). Effects of

626   snow cover on the timing and success of reproduction in high-Arctic pink-footed geese

627   Anser brachyrhynchus. *Polar Biology*, 30, 1363-1372.

628 Maldonado-Chaparro, A.A., Blumstein, D.T., Armitage, K.B. & Childs, D.Z. (2018). Transient

629   LTRE analysis reveals the demographic and trait-mediated processes that buffer

630   population growth. *Ecology letters*, 21, 1693-1703.

631 McCarthy, M.A. & Masters, P. (2005). Profiting from prior information in Bayesian analyses of

632   ecological data. *Journal of Applied Ecology*, 42, 1012-1019.

633 McLean, N., Lawson, C.R., Leech, D.I. & van de Pol, M. (2016). Predicting when climate-driven

634   phenotypic change affects population dynamics. *Ecology Letters*, 19, 595-608.

635 McLean, N.M., van der Jeugd, H.P., Van Turnhout, C.A., Lefcheck, J.S. & Van de Pol, M.

636   (2020). Reduced avian body condition due to global warming has little reproductive or

637   population consequences. *Oikos*.

638 Menu, S., Gauthier, G. & Reed, A. (2005). Survival of young greater snow geese (Chen

639   caerulescens atlantica) during fall migration. *The Auk*, 122, 479-496.

640 Metcalf, C.J.E., Ellner, S.P., Childs, D.Z., Salguero-Gómez, R., Merow, C., McMahon, S.M. *et*

641   *al.* (2015). Statistical modelling of annual variation for inference on stochastic population

642   dynamics using Integral Projection Models. *Methods in Ecology and Evolution*, 6, 1007-

643   1017.

644 Owen, M. & Black, J.M. (1989). Factors affecting the survival of Barnacle Geese on migration

645   from the breeding grounds. *Journal of Animal Ecology*, 58, 603-617.

646 Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E. *et al.* (2010).

647   Coupled dynamics of body mass and population growth in response to environmental

648   change. *Nature*, 466, 482.

649 Ozgul, A., Tuljapurkar, S., Benton, T.G., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T.

650   (2009). The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda.

651   *Science*, 325, 464-467.

652 Paniw, M., James, T., Archer, C.R., Roemer, G., Levin, S., Compagnoni, A. *et al.* (2019a).

653   Global analysis reveals complex demographic responses of mammals to climate change.

654   *bioRxiv*.

655   Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T. & Ozgul, A. (2019b). Life history responses

656   of meerkats to seasonal changes in extreme environments. *Science*, 363, 631-635.

657   Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009). Nutrition integrates environmental

658   responses of ungulates. *Functional ecology*, 23, 57-69.

659   Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev.*

660   *Ecol. Evol. Syst.*, 37, 637-669.

661   Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.M., Delorme, D., Warnant, C. *et al.* (2014).

662   Mismatch between birth date and vegetation phenology slows the demography of roe

663   deer. *PLoS biology*, 12.

664   Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.M., Douhard, M., Klein, F. *et al.* (2015). The

665   influence of birth date via body mass on individual fitness in a long-lived mammal.

666   *Ecology*, 96, 1516-1528.

667   Plummer, M. (2013). rjags: Bayesian graphical models using MCMC. *R package version*, 3.

668   Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an

669   Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal*

670   *Society of London B: Biological Sciences*, 363, 2367-2373.

671   Post, E. & Stenseth, N.C. (1999). Climatic variability, plant phenology, and northern ungulates.

672   *Ecology*, 80, 1322-1339.

673   Post, E., Stenseth, N.C., Langvatn, R. & Fromentin, J.-M. (1997). Global climate change and

674   phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of*

675   *London. Series B: Biological Sciences*, 264, 1317-1324.

676   Reed, A. & Plante, N. (1997). Decline in body mass, size, and condition of greater snow geese,

677   1975-94. *The Journal of wildlife management*, 413-419.

678   Reed, E.T., Gauthier, G. & Giroux, J.-F. (2004). Effects of spring conditions on breeding

679   propensity of greater snow goose females. *Animal Biodiversity and Conservation*, 27, 35-

680   46.

681   Rees, M. & Ellner, S.P. (2009). Integral projection models for populations in temporally varying

682   environments. *Ecological Monographs*, 79, 575-594.

683   Sainmont, J., Andersen, K.H., Varpe, Ø. & Visser, A.W. (2014). Capital versus income breeding

684   in a seasonal environment. *The American Naturalist*, 184, 466-476.

685   Schamber, J.L., Esler, D. & Flint, P.L. (2009). Evaluating the validity of using unverified indices

686   of body condition. *Journal of Avian Biology*, 40, 49-56.

687   Schaub, M., Jakober, H. & Stauber, W. (2013). Strong contribution of immigration to local

688   population regulation: evidence from a migratory passerine. *Ecology*, 94, 1828-1838.

689   Scheffer, M., Straile, D., van Nes, E.H. & Hosper, H. (2001). Climatic warming causes regime

690   shifts in lake food webs. *Limnology and Oceanography*, 46, 1780-1783.

691   Schmutz, J.A. (1993). Survival and pre-fledging body mass in juvenile Emperor Geese. *The*

692   *Condor*, 95, 222-225.

693   Serreze, M.C. & Barry, R.G. (2011). Processes and impacts of Arctic amplification: A research

694   synthesis. *Global Planetary Change*, 77, 85-96.

695   Sæther, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores:

696   a search for mechanisms. *Trends in Ecology and Evolution*, 12, 143-149.

697   Sæther, B.-E., Visser, M.E., Grøtan, V. & Engen, S. (2016). Evidence for r-and K-selection in a

698   wild bird population: a reciprocal link between ecology and evolution. *Proceedings of the*

699   *Royal Society B: Biological Sciences*, 283, 20152411.

700 Tuljapurkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary

701   dynamics of r-selection. *Theoretical Population Biology*, 21, 141-165.

702 Varpe, Ø., Jørgensen, C., Tarling, G.A. & Fiksen, Ø. (2009). The adaptive value of energy

703   storage and capital breeding in seasonal environments. *Oikos*, 118, 363-370.

704 Visser, M.D., Bruijning, M., Wright, S.J., Muller-Landau, H.C., Jongejans, E., Comita, L.S. *et*

705   *al.* (2016). Functional traits as predictors of vital rates across the life cycle of tropical

706   trees. *Functional Ecology*, 30, 168-180.

707 White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of

708   marked animals. *Bird study*, 46, S120-S139.

709 Wilson, S. & Arcese, P. (2003). El Nino drives timing of breeding but not population growth in

710   the song sparrow (Melospiza melodia). *Proceedings of the National Academy of*

711   *Sciences*, 100, 11139-11142.

712