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RESEARCH ARTICLE

Context-dependent fitness costs of reproduction despite stable body mass costs in an Arctic herbivore

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Abstract

1. The cost of reproduction on demographic rates is often assumed to operate through changing body condition. Several studies have found that reproduction depresses body mass more if the current conditions are severe, such as high population densities or adverse weather, than under benign environmental conditions. However, few studies have investigated the association between the fitness components and body mass costs of reproduction.
2. Using 25 years of individual-based capture–recapture data from Svalbard reindeer *Rangifer tarandus platyrhynchus*, we built a novel Bayesian state-space model that jointly estimated interannual change in mass, annual reproductive success and survival, while accounting for incomplete observations. The model allowed us to partition the differential effects of intrinsic and extrinsic factors on both non-reproductive mass change and the body mass cost of reproduction, and to quantify their consequences on demographic rates.
3. Contrary to our expectation, the body mass cost of reproduction (mean = -5.8 kg) varied little between years (CV = 0.08), whereas the between-year variation in body mass changes, that were independent of the previous year's reproductive state, varied substantially (CV = 0.4) in relation to autumn temperature and the amount of rain-on-snow in winter. This body mass loss led to a cost of reproduction on the next reproduction, which was amplified by the same environmental covariates, from a 10% reduction in reproductive success in benign years, to a 50% reduction in harsh years. The reproductive mass loss also resulted in a small reduction in survival.
4. Our results show how demographic costs of reproduction, driven by interannual fluctuations in individual body condition, result from the balance between body

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mass costs of reproduction and body mass changes that are independent of previous reproductive state. We illustrate how a strong context-dependent fitness cost of reproduction can occur, despite a relatively fixed body mass cost of reproduction. This suggests that female reindeer display a very conservative energy allocation strategy, either aborting their reproductive attempt at an early stage or weaning at a relatively constant cost. Such a strategy might be common in species living in a highly stochastic and food limited environment.

KEYWORDS

Arctic, Bayesian statistics, Capture–Mark–Recapture, imputation, reindeer, reproductive success, survival, time-varying individual covariate

1 | INTRODUCTION

The concept of a ‘cost of reproduction’ encompasses any physiological, ecological or behavioural consequence of an individual's reproductive effort that may subsequently have a negative impact on the individual or its offspring. Initially, the idea was developed within the theory of energy allocation (Williams, 1966), since investment of energy in reproduction was expected to cause reduced investment of energy in the body's energetic reserves (Fisher, 1930; Tuomi et al., 1983). This energy allocation model of the costs of reproduction is still dominant, even though other physiological mechanisms are also at play (Plumel et al., 2014; Zhang & Hood, 2016). Today, an extensive literature documents costs of reproduction on a range of traits, in both animals and plants, including measures of immune function (Harshman & Zera, 2007; Schwenke et al., 2016), body composition (Golet & Irons, 1999; Primack & Hall, 1990), future reproductive success (Bowers et al., 2012; Nilsson & Svensson, 1996) and survival (Aragón et al., 2009; Descamps et al., 2009; Martin, 1995). A cost of reproduction generates a trade-off between current reproduction and future fitness and is at the core of the evolutionary theory of life histories (Stearns, 1992). Furthermore, it has been shown that this trade-off can be affected by a multitude of ecological factors that vary between species, as well as within species, in space and time (Festa-Bianchet et al., 2019; Hamel, Gaillard, et al., 2010).

Ungulates are long-lived and risk averse when it comes to jeopardizing their own survival (Bårdsen et al., 2008). Accordingly, meta-studies have found that the costs of reproduction typically has a stronger effect on the next reproductive event than future survival in large and long-lived mammals (Hamel, Gaillard, et al., 2010). Festa-Bianchet et al. (1998) demonstrated that the costs of reproduction for subsequent demographic rates increased under less favourable environmental conditions in bighorn sheep *Ovis canadensis*. The pattern of low costs of reproduction when resources are plentiful, and high costs of reproduction when resources are limited has been confirmed in several studies of ungulate populations (Milner et al., 2013; Moyes et al., 2006; Tavecchia

et al., 2005). In many instances, body condition and environment were proposed as the main driver of the costs of reproduction and its effects on demographic rates (Bårdsen & Tveraa, 2012; Festa-Bianchet et al., 1998, 2019; Milner et al., 2013). However, we still have a poor understanding of how environmental conditions modulate this trade-off through effects on between-year variation in mass unrelated to reproduction, hereafter referred to as non-reproductive mass change, and loss of mass due to the costs of reproduction. Understanding the interaction between environment and life-history trade-off is highly relevant given the increasingly variable climate.

Here, we use 25 years of individual-based data on Svalbard reindeer *Rangifer tarandus platyrhynchus*, to explore the energy allocation model of costs of reproduction in a capital breeder (Barboza & Parker, 2008). The Svalbard reindeer is a particularly suitable species for this analysis. While it shows large variation in body mass within year like many ungulate (Albon et al., 2017; Pelletier et al., 2007), it also shows large interannual variation in body mass. Furthermore, body mass is depressed by reproduction, and is a main predictor of demographic rates and population dynamics (Albon et al., 2017; Veiberg et al., 2017). The main environmental drivers affecting body mass variations are autumn temperatures and early snowfall (Loe et al., 2021), winter weather (rain-on-snow [ROS] events) and population density (Albon et al., 2017; Hansen et al., 2019). We estimate the body mass changes associated with reproduction and explore to what degree, and how, these costs vary between years in relation to environmental conditions, and how this translates into fitness costs of reproduction.

Joint modelling of growth, reproduction and survival has profited from recent methodological advances (e.g. Reinke et al., 2020; Smout et al., 2020). We develop a dynamic state-space model where individual body mass change from one year to the next with net body mass change modelled as an additive function of non-reproductive body mass change and body mass cost of reproduction. This flexible modelling approach allows both extrinsic covariates characterizing the environment, as well as intrinsic covariates, including age, previous body mass and reproductive

state, to be included as predictor variables of body mass change. Similarly, the sub-models for survival and reproductive success included both extrinsic and intrinsic predictor variables, as well as individual body mass (Figure 1), and therefore were dynamically linked to the body mass sub-models. Our novel integrated modelling approach allows a holistic evaluation of costs of reproduction in the study organism, and the pathways of environmental modulation of fitness costs of reproduction.

2 | MATERIALS AND METHODS

2.1 | Study population

The Svalbard reindeer population in Nordenskiöld Land, Svalbard (77°50'–78°20'N, 15°00'–17°30'E), was studied in and around the valleys of Reindalen, Semmeldalen and Colesdalen where individual-based monitoring has been conducted, uninterrupted since 1995 (Albon et al., 2017). Up to 2019, a total of 815 individual females have been caught during late winter (mostly April; range: mid-March to early May), using a net stretched between two snowmobiles (Omsjoe et al., 2009). New individuals were marked mainly in their first year of life (c. 10 months of age) using coloured and numbered

plastic ear tags and collars and were hence of known age. Captured females were weighed to the nearest 0.5 kg and the dataset includes on average 4 annual body mass measurements per individual ($SD = 2.2$, range = 1–12) over their lifetime yielding a total of 2,801 mass estimates across these individuals. All capture and live animal handling procedures were performed under licenses from the Norwegian Food Inspection Authority and its predecessor, the Norwegian National Research Authority.

In summer, surveys were conducted by two or more observers using binoculars and telescopes, between 24 June and 25 August to assess the presence or absence of a calf associated with marked females. Average group size in summer is only 2–3 individuals (Loe et al., 2006) facilitating assignment of mother–calf pairs. Since Svalbard consists of open landscapes, animals can be easily spotted and identified at long distances (>1 km). When a female was observed with a calf at heel during the summer census, it was classified as a successful reproduction (965 successful vs. 1596 unsuccessful; Figure S1).

2.2 | Environmental variables

Svalbard reindeer inhabit a highly seasonal environment that has been heavily impacted by global warming (Førland et al., 2011; Hansen et al., 2014; Van der Wal & Stien, 2014). Both the January and July daily mean temperatures at Svalbard Airport (seklima.met.no) increased significantly between 1995 and 2017 ($0.44 \pm 0.16^\circ\text{C}$ per annum and $0.073 \pm 0.027^\circ\text{C}$, respectively; Albon et al., 2017). Increased winter temperatures has led to more ROS events in later years, causing winter feeding sites to be ice-locked (Albon et al., 2017; Peeters et al., 2019). Despite an increasing frequency of ROS events, the population size of Svalbard reindeer has doubled in the past 20 years (Albon et al., 2017; Hansen et al., 2019).

We quantified ROS as the total rainfall occurring on days with mean temperatures above 0°C during the months of November–March. We quantified autumn environmental conditions using October degree-days for days with average temperature $>0^\circ\text{C}$. ROS and October degree-days were log transformed. Annual summer environmental conditions were quantified using mean daily June–July temperature, which strongly influences peak plant biomass and consequently forage availability (Van der Wal & Stien, 2014). Also, we investigated the negative effect of high population size on the costs of reproduction. Population size estimates were obtained from an integrated population model (Lee et al., 2015). The estimated number of females and calves during the study period ranged from 767 (1996) to 2,265 (2018). Population size estimates were detrended prior to the analysis to account for increasing carrying capacity (Hansen et al., 2019), associated with warmer summers and higher primary productivity, based on a linear regression model of population size as a function of year. All environmental variables were centred and scaled to a standard deviation of 1 to facilitate model convergence and parameter comparisons.

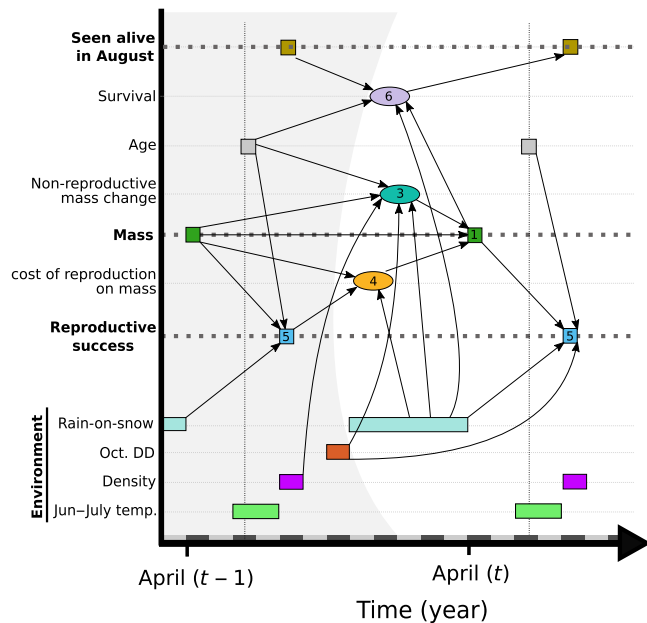


FIGURE 1 Conceptual framework of the statistical model. The x-axis shows time. The observable reindeer state variables, body mass, reproductive success (calf at heel) and the observation of a live animal, are shown as squares and written in bold. Ovals (non-reproductive mass change, body mass cost of reproduction, survival) show the latent variables. Arrows show significant relationship that were kept in the final model. Vertical dotted lines indicate the calving period while the grey shaded region highlights variables considered to affect next year latent variables ($t + 1$) as opposed to same year (t). The numbers refer to the specific equations in the text describing these components

2.3 | Interannual change in body mass

Ignoring detection probabilities of <1 can lead to biased parameter estimates and erroneous inferences (Gimenez et al., 2008). A Bayesian hierarchical modelling approach can both account for imperfect detection and allow for model based imputation of the states of animals (mass, reproductive status or survival) when they were not observed (Bonner et al., 2010; King et al., 2008; Smout et al., 2020). In our model, body mass was a main time-varying individual state variable that varied from one year to the next according to:

$$w_{i,t} = w_{i,t-1} + l_{i,t} + (C_{i,t} * R_{i,t-1}) + \epsilon_{i,t}, \quad (1)$$

where the body mass ($w_{i,t}$) of individual i in year t is modelled as a function of (a) the body mass the previous year ($w_{i,t-1}$), (b) an annual non-reproductive body mass change ($l_{i,t}$), (c) an additive body mass cost of reproduction ($C_{i,t}$) resulting in mass loss in the year from $t-1$ to t due to successful reproduction in year $t-1$ (the indicator variable $R_{i,t-1}$ coded as 1 for successful reproduction and 0 for unsuccessful reproduction in year $t-1$), and (d) process error associated with body mass change from year $t-1$ to t ($\epsilon_{i,t}$). The individual- and occasion-specific process errors in the change in mass were assumed to be normally distributed, $\epsilon_{i,t} \sim N(0, \sigma_\epsilon)$. In order for the model to be identifiable, we assume that the individual and time variations are additive. Variation in the dataset with respect to the date at which individuals were captured and weighed (range from 12 March to 8 May) was accounted for by assuming a linear seasonal loss in mass. The expected body mass ($w_{i,t}$) was estimated conditional on the observed measurement of body mass ($o_{i,t}$) and assuming a linear decrease in late winter body mass with the Julian capture day:

$$o_{i,t} = w_{i,t} + \beta^d \times d_{i,t} + \delta_{i,t}, \quad (2)$$

assuming the observation error $\delta_{i,t} \sim N(0, \sigma_\delta)$, and $w_{i,t}$, β^d and σ_δ being parameters estimated from data. Body mass observations ($o_{i,t}$) were scaled prior to modelling by subtracting the mean and dividing by the standard deviation (mean = 42.5 kg, $SD = 12.7$). The expected body mass ($w_{i,t}$) on the 18th of April (the average capture date) was used as our measure of annual body mass change in the model (Equation 1). Body mass at 10 months old (age = 0) represented initial body mass values ($w_{i,t=1}$) for the individuals and were either estimated from direct measurements during capture ($o_{i,t}$, Equation 2) or, when missing (20% of individual), drawn from a normal distribution with parameters based on available observations (w_0 , σ_{w0} ; Table S1).

The model for non-reproductive mass change ($l_{i,t}$ in Equation 1) included both extrinsic and intrinsic drivers:

$$l_{i,t} = f(A_{i,t}) + \sum_{h=1}^p X_{h,i,t} \beta_h^l + d_i^l + e_t^l, \quad (3)$$

where $f(A_{i,t})$ is a nonlinear function describing body mass change with age described below, $\sum_{h=1}^p X_{h,i,t} \beta_h^l$ is a linear model for the impact

on body mass growth of the h^{th} predictor variable ($X_{h,i,t}$) for individual i at time t and β_h^l is the associated regression coefficient. The model included additive random effects to describe both individual ($d_i^l \sim N(0, \sigma_{d,l})$) and between-year ($e_t^l \sim N(0, \sigma_{e,l})$) variation in body mass change not accounted for by the fixed effects predictors ($f(A_{i,t}) + (\sum_{h=1}^p X_{h,i,t} \beta_h^l)$ in Equation 3). Predictor variables included as linear fixed effects in Equation 3 were ROS_t , October degree-days $_{t-1}$, June–July temperature $_{t-1}$, population size $_{t-1}$ and previous body mass ($w_{i,t-1}$). We also evaluated potential interaction effects between environmental variables and previous body mass and between ROS and population size by including their product (Hansen et al., 2019). Overall between-year variability in l was estimated by $\sigma_{e,l}$ using Equation 3 without any environmental covariates. To facilitate interpretation, $\sigma_{d,l}$ and $\sigma_{e,l}$ were back transformed into the original kilogram scale by multiplying by the standard deviation used to scale body mass ($\zeta_{d,l} = \sigma_{d,l} \times 12.7$ and $\zeta_{e,l} = \sigma_{e,l} \times 12.7$, respectively).

Like most ungulates, reindeer body mass changes in three distinct phases linked to age: a phase of intense growth in early life, a phase of stable mass at prime age and phase of body mass loss associated with senescence in body condition of older individual (Myrsterud et al., 2001). Some of the variability associated with age was captured by including previous body mass as a predictor of body mass change (see above). However, additional variation in growth with age was apparent. We used a threshold model for this nonlinear age component $f(A_{i,t})$ in our model for non-reproductive mass change (Equation 3) as it can provide an adequate description of the nonlinear pattern with age (Weladji et al., 2010). The age model ($f(A_{i,t})$) had two break points estimated from the data. Non-reproductive mass change for a given mass increased linearly with age ($a2$) until the first break point (*prime*; constrained to be between 3 and 8 years of age), representing the start of prime age. During prime age, the effect of age remained constant until the second breakpoint (*old*; constrained to be between 8 and 13), representing the start of senescence. After the second breakpoint, non-reproductive mass change decreased linearly causing a decrease in mass at old age ($a3$). Posterior checks showed a lack of fit for early non-reproductive mass change; therefore, we added a parameter ($a1$) to allow a different mass change from 0 to 1 year old. This resulted in a functional form for age-specific net change in mass that fitted the data well (Figure S9).

The mass cost of reproduction, $C_{i,t}$, was assumed to depend linearly on the environmental variables. We also tested for effects of maternal condition by including an effect of previous body mass (Macdonald et al., 2020). The cost of reproduction on mass was therefore defined as:

$$C_{i,t} = \sum_{h=1}^p X_{h,i,t} \beta_h^C + d_i^C + e_t^C, \quad (4)$$

where β_h^C is the regression coefficient estimated from data. The predictor variables ($X_{h,i,t}$) included ROS_t , October degree-days $_{t-1}$, June–July temperature $_{t-1}$, population size $_{t-1}$ and previous body mass ($w_{i,t-1}$). We also tested for interactions between environmental variables and

previous body mass and the interaction between ROS and population size by including their product. To account for individual variation in maternal investment and annual variation in the cost of producing a calf on mass, the model included additive random effects for between individual ($d_i^C \sim N(0, \sigma_{d,C})$) and year ($e_t^C \sim N(0, \sigma_{e,C})$) variability. Overall between-year variability in C was estimated by $\sigma_{e,C}$ using Equation 3 without any environmental covariates fitted. To facilitate interpretation, $\sigma_{d,C}$ and $\sigma_{e,C}$ were back transformed into the original kilogram scale by multiplying by the standard deviation used to scale body mass ($\zeta_{d,C} = \sigma_{d,C} \times 12.7$ and $\zeta_{e,C} = \sigma_{e,C} \times 12.7$, respectively).

2.4 | Model of reproductive success

Reproductive success in female reindeer is mainly determined by age and body mass (Albon et al., 2017) but may also decrease under harsh environmental conditions, such as high ROS (Douhard et al., 2016). The change in reproductive success with age, independent of body mass, could reflect either change in experience (Barbraud & Weimerskirch, 2005), development or senescence (Lemaître & Gaillard, 2017). In addition, we also evaluated a direct effect of previous reproductive success independent of effects operating through changes in April mass, on subsequent reproductive success. Such a direct effect was expected to be negative (Harshman & Zera, 2007); but see Weladji et al. (2008) for an example of a positive relationship between subsequent reproductive events. The probability to have a calf at heel in August ($p_{i,t}$) was modelled using a generalized linear mixed model with a logit link function:

$$\text{logit}(p_{i,t}) = \sum_{h=1}^p X_{h,i,t} \beta_h^R + d_i^R + e_t^R, \quad (5)$$

where β_h^R is the regression coefficient estimated from the data. Fixed effects included a linear model for age modelled as a categorical variable with age the classes 2, 3, 4–5, 6–9 and 10+ years old, the production of a calf during the previous reproductive season ($R_{i,t-1}$), body mass the same year ($w_{i,t}$) and the environmental variables ROS_t, October degree-days_{t-1}, June–July temperature_t and population size_{t-1}. We tested for potential interactions between body mass and environmental variables and the interaction between ROS and population size by including their product. In addition, we included individual ($d_i^R \sim N(0, \sigma_{d,R})$) and year ($e_t^R \sim N(0, \sigma_{e,R})$) random effects to account for non-independence and residual individual and annual variability. Realized reproductive success ($R_{i,t}$; either 0 or 1) was assumed to follow a Bernoulli distribution with probability $p_{i,t}$; $R_{i,t} \sim \text{Bernoulli}(p_{i,t})$.

2.5 | Survival model

Because of imperfect detection (Lebreton et al., 1992), annual survival from one August to the next was estimated using a state-space formulation of the Cormack–Jolly–Seber model with a time-varying individual covariate (King et al., 2008). Using a logit link function,

sighting probability was allowed to vary between years using a random effect specification (Lee et al., 2015). The effect of reproductive state on sighting probability was tested but found not to be significant. The survival s from August $t-1$ to t of individual i varied with years t , such that:

$$\text{logit}(s_{i,t}) = \left(\sum_{h=1}^p X_{h,i,t} \beta_h^S \right) + e_t^S, \quad (6)$$

where β_h^S is the regression coefficient estimated by data. Explanatory linear predictor variables included age, body mass ($w_{i,t}$), ROS_t and population size_{t-1}. Between-year variation not accounted for by the linear fixed effect model was modelled by the random effect. Following Lee et al. (2015), we modelled age using six age classes: 0, 1, 2, 3–8, 9–11 and 12+ year olds. Realized survival ($S_{i,t} \in [0, 1]$) was assumed to follow a Bernoulli distribution with probability $s_{i,t}$; $S_{i,t} \sim \text{Bernoulli}(s_{i,t})$.

2.6 | Model implementation and fitting

We implemented our model in JAGS (Plummer, 2010) using the R2JAGS package (Su & Yajima, 2015) in R (R Core Team, 2017), setting 200,000 iterations with a thinning of 150 and a burn-in of 50,000 iterations (see Supporting Information for the full script). We assessed convergence visually and using Gelman and Rubin's convergence diagnostic (Gelman & Rubin, 1992). The model structure was simplified sequentially by removing non-significant predictor variables from the full model (predictor variables with 95% credible intervals for parameter estimates overlapping zero). The model covered individual states over the entire life of the animals (from first capture at 10 months old until death). If an animal was not observed in a given year, its body mass and/or calving status was unknown and imputed based on previous state, next state and current environment. In a Bayesian framework, imputed values (sighting probability is of 43 [38, 48]%) are estimated model parameters just like regression coefficients (Bonner et al., 2010). The identifiability of model parameters can be an issue when fitting complex models. Therefore, we used a simulation to generate synthetic data and assessed the bias and the 95% coverage (see further explanation and the script to run the simulation and the estimation of the bias in the Supporting Information section 2. Assessment of coverage is approximate since only 15 replicates were used due to time constraint). Fitting the model to synthetic datasets suggests that all parameters were identifiable with a minimum bias, and not an artefact of the constraints in the model. Model fit was also assessed by k -fold cross-validation, with $k = 5$, resulting in a cross-validated R square of 0.71 for body mass. Throughout the text, parameter estimates and posterior predictions are reported with their 95% credible intervals as posterior mean [95% CI].

2.7 | Indirect effect of previous reproduction

In our initial model, the cost of reproduction on next year's reproduction and survival can be realized both through a direct effect

and through the body mass effect since mass is an important determinant of both reproductive success and survival. To quantify this indirect cost of reproduction on subsequent reproduction and survival through mass change, we estimated the expected annual body mass of individuals with and without previous reproductive success ($R_{i,t-1} = 0, 1$) and compared the associated estimates of expected subsequent reproductive success and survival.

3 | RESULTS

3.1 | Interannual change in mass

Female Svalbard reindeer show remarkable variation in body mass from one April to the next (5% and 95% percentile of net mass change in prime-aged individuals are -12 and $+15$ kg, respectively). The estimated between-year variation in non-reproductive mass change (l in Equation 3) for a 7-year-old female of average body mass (52 kg) showed a range of values from -3 to 12 kg (mean = 4.0 kg, $\zeta_{e,l} = 4.0$; Figure 2). The body mass cost of reproduction was substantial (mean = -5.8 kg) but varied little between years (range = -7 to -5 kg; $\zeta_{e,C} = 0.7$; Figure 2). Nevertheless, this relatively stable body mass cost of reproduction contributed to observed between-year variation in average net body mass change due to highly variable reproductive rates (mean = 58% ; range: 9% – 92%).

Partitioning of the causes of variation in non-reproductive mass change showed that intrinsic factors were important. Both individual body mass at time $t - 1$ and age were important determinants

of interannual changes in mass (Table 1; Table S1). Light individuals tended to increase in mass, while heavy individuals tended to show a decrease in mass (Figure 3). Maximum non-reproductive mass change was reached at 6 years of age [5.3, 6.4], and senescence was detected after the age of 10.5 [9.8, 11.5] years (Table S1). The combined effect of mass-dependent body mass change and age-dependent body mass change resulted in a high expected mass change in growing young individuals, a fairly stable body mass change in 4 to 9 years old, and a decline in average body mass change with age above the age of 9 (Figure S2; Table 1; Table S1). The model also suggested substantial individual variation in average mass change ($\zeta_{d,l} = 2.1$ [1.8, 2.4] kg).

Extrinsic environmental variables accounted for substantial interannual variation in non-reproductive mass change (Table 1; Figure 2). There was evidence for effects of ROS_t , October degree days $_{t-1}$ and population size $_{t-1}$, but not June–July temperature $_{t-1}$, on the annual variation in non-reproductive body mass change (Table 1). Body mass change was higher in years with high values for October degree days (Table 1; Figure 3a), and also higher in years with low ROS (Table 1; Figure 3b). In addition, the negative effect of ROS was stronger when reindeer population size was moderate or high (Table 1; Figure 3b), a situation likely to represent intensified forage competition. The interaction effect between population size and previous body mass was also significant, with a smaller effect of previous body mass at high population sizes (Table 1). The autumn temperature effect also depended on previous body mass (Table 1), with warm autumns leading to a slightly larger gain in body mass for previously heavy individuals, compared to lighter individuals. Additional between-year variation in mass change ($\zeta_{e,l} = 3.2$ [2.3,

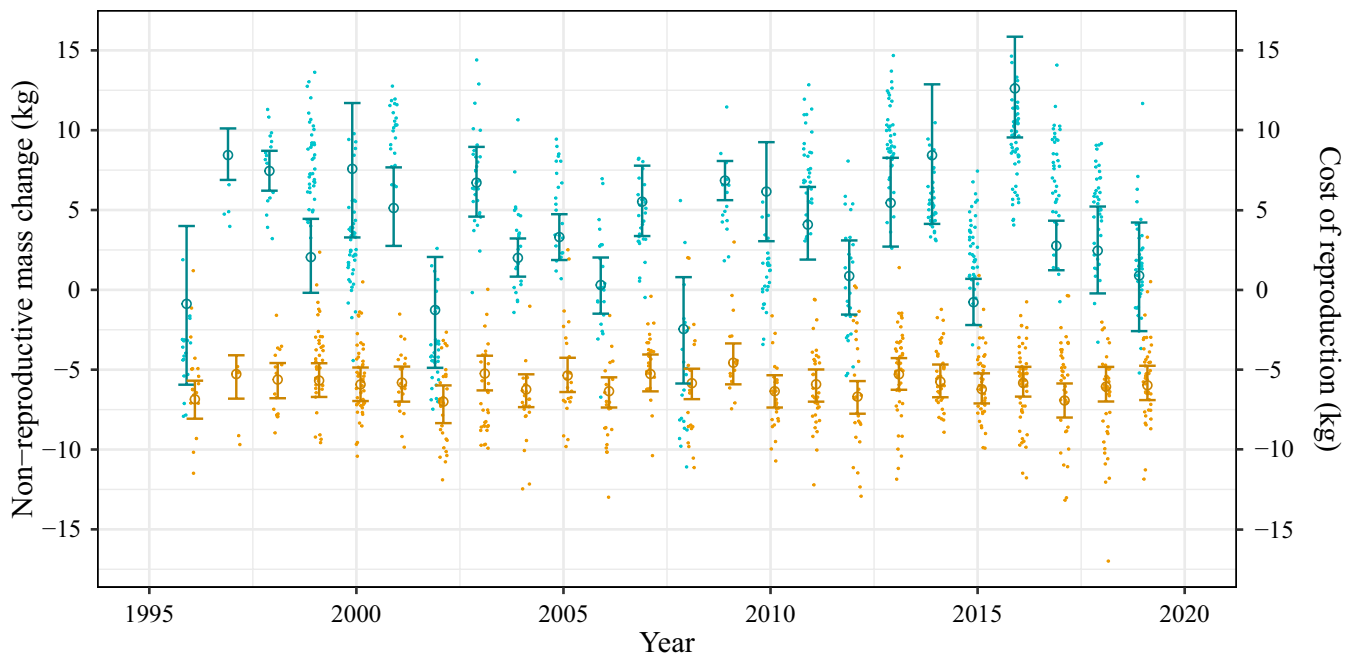


FIGURE 2 Non-reproductive mass change (green) and body mass cost of reproduction (orange) for an average 7-year-old Svalbard reindeer each year of the study period (1996–2019). Orange small dots show observed mass change for non-reproducing individual (corrected for age and previous body mass) while small green dots show observed mass change for reproducing individuals minus their predicted non-reproductive mass change

TABLE 1 Effect (mean and 95% credible interval) of environment, mass and previous reproductive success variables on mass change, probability to have a calf and survival probability, respectively, in Svalbard reindeer between years 1995 and 2019. Dashes show parameters which were not tested. N.S. denotes parameters which were not significant and removed from the model. Top four lines give random effect estimates of standard deviations (σ), subsequent lines give fixed effect estimates (β). Mass refers to previous mass ($w_{i,t-1}$) in the model for mass change (Equations 3 and 4) and mass same year ($w_{i,t}$) in the models for reproductive success (Equation 5) and survival (Equation 6)

Parameter	Mass change (w)	Reproductive success (p)	Survival (s)
$\sigma_{d,l}$	0.17 [0.14, 0.19]	0.95 [0.71, 1.21]	—
$\sigma_{e,l}$	0.25 [0.18, 0.36]	0.28 [0.04, 0.53]	0.90 [0.71, 1.00]
$\sigma_{d,c}$	0.09 [0.03, 0.15]	—	—
$\sigma_{e,c}$	0.03 [0.00, 0.08]	—	—
Intercept (prime-age)	0.80 [0.69, 0.92]	-1.52 [-1.98, -1.10]	2.94 [2.42, 3.45]
Mass	-0.65 [-0.73, -0.58]	3.36 [2.80, 4.00]	0.66 [0.19, 1.14]
Pop. Size	-0.07 [-0.18, 0.05]	N.S.	N.S.
Rain-on-snow	-0.17 [-0.31, -0.04]	-0.72 [-1.11, -0.36]	-0.42 [-0.86, 0.01]
Oct. degree days	0.17 [0.05, 0.30]	0.70 [0.35, 1.05]	N.S.
Pop. size: Mass	-0.02 [-0.04, -0.01]	N.S.	N.S.
Oct. degree days: Mass	0.03 [0.01, 0.05]	0.48 [0.02, 0.94]	N.S.
Rain-on-snow: Mass	N.S.	-0.64 [-1.07, -0.23]	N.S.
Rain-on-snow : Pop. size	-0.03 [-0.15, 0.08]	N.S.	N.S.
R_{t-1} : Intercept	-0.36 [-0.42, -0.29]	N.S.	N.S.
R_{t-1} : Mass	-0.13 [-0.20, -0.06]	—	—
R_{t-1} : Rain-on-snow	-0.04 [-0.08, 0.01]	—	—

4.6] kg) indicates that additional environmental factors may affect change in body mass but were not captured by the environmental variables we measured.

There was some evidence for the body mass cost of reproduction to be affected by extrinsic factors, as there was a slight decrease in the body mass cost of reproduction with increasing ROS values (Table 1; Figure 3b). However, the effect of ROS on the body mass cost of reproduction (C in Equation 4) was small, compared to the effect of ROS, on non-reproductive body mass change (I in Equation 3), and none of the other environmental variables evaluated showed strong evidence of an effect on body mass cost of reproduction (Table S2). However, the body mass cost of reproduction was affected by the previous body mass of the individual, being higher for previously heavy individuals than lighter conspecifics (Table 1; Figure 3). There was evidence for additional individual variation in the body mass cost of reproduction, unexplained by the fixed effect model (Table 1; $\zeta_{d,c} = 1.2$ [0.4, 1.9] kg).

The net change in mass from one April to the next results from the balance of the non-reproductive mass change (Equation 3) and the body mass cost of reproduction (Equation 4). For example, in a year with high October degree days, an average 7 year old is expected to show a limited loss of -1.3 [-3.8, 0.9] kg mass following successful reproduction and to gain 4.4 [1.9, 6.8] kg if not reproducing (Figure S3a). In contrast, in a year with average October

degree days, successful reproduction is expected to depress subsequent body mass by -4.1 [-5.6, -2.6] kg, while no reproduction would result in an increase in mass of 1.7 [0.1, 3.2] kg. Finally, harsh years, with low October degree days, will lead to a decrease of -7.9 [-10.7, -5.2] kg mass in reproducing females but little change in non-reproducing females (mean = -2.1 [-4.9, 0.5] kg).

Through its influence on non-reproductive mass change, previous mass ($w_{i,t-1}$) also had an impact on the net change in body mass. The heaviest females lost on average as much as 12.9 [9.4, 16.5] kg following reproduction (Figure S3a). In contrast, forgoing reproduction led to an expected increase in mass of 14.3 [10.7, 17.8] kg for the lightest 7 year olds following benign winter conditions, while heavy females under similar conditions were expected to gain 4.9 [1.2, 8.5] kg. Similar patterns were observed for ROS (Figure S3b). In years of low ROS, an average 7 year old is expected to maintain its mass following successful reproduction (mean = -0.5 [-3.4, 2.2] kg) and gain mass if not reproducing (mean = 4.6 [1.8, 7.4] kg). However, in an average and high ROS year, successful reproduction is expected to cause a body mass loss of -4.7 [-6.2, -3.2] kg, and -7.3 [-9.8, -5.0] kg, respectively. If no reproduction took place, however, females are expected to show no significant loss of body mass in either an average (mean = 1.2 [-0.3, 2.8] kg) or a high ROS year (mean = -1.0 [-3.5, 1.4] kg). Consequently, mass in April can vary widely depending on reproductive status the previous year and environmental conditions (Figure 4a,c).

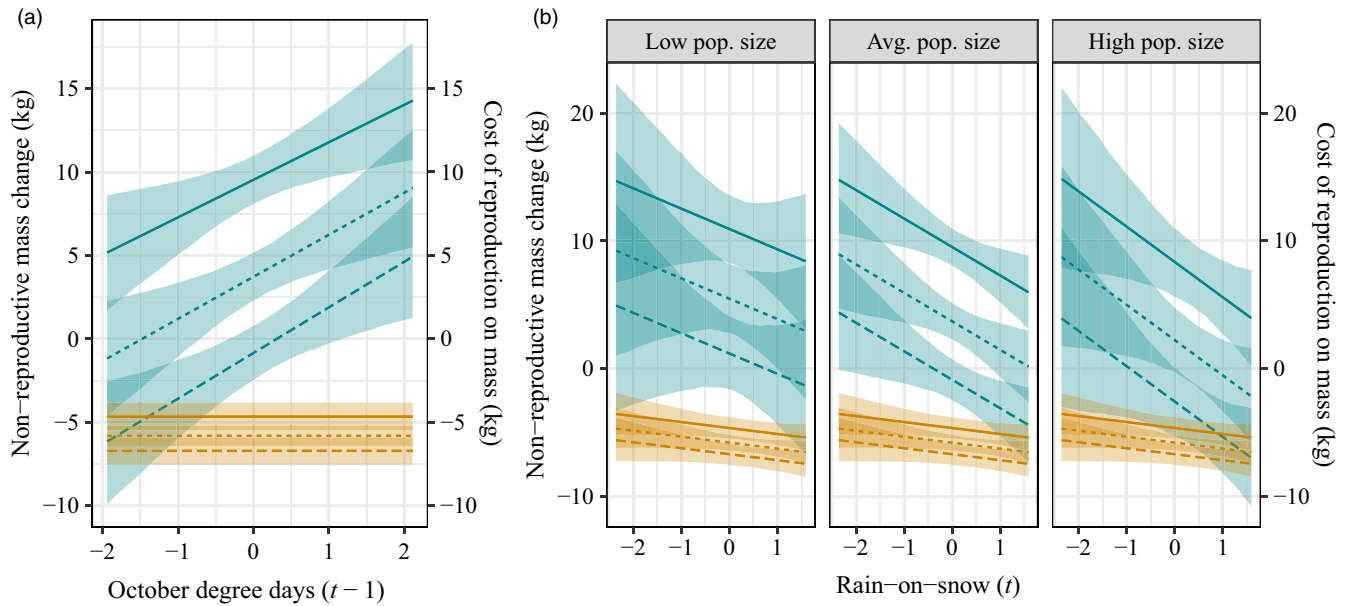


FIGURE 3 Predicted non-reproductive mass change (green) and body mass cost of reproduction (orange) as a function of previous body mass and environment for an average 7-year-old Svalbard reindeer. Panel (a) illustrates the effect of October degree days. Panel (b) illustrates the effect of rain-on-snow and its interaction with population size. Solid, dotted and dashed lines represent light (10th percentile), average and heavy (90th percentile) individuals, respectively

3.2 | Determinants of reproductive success

The probability of having a calf at heel in August was highly dependent on age (Table S1; Figure S9b) and April body mass (Table 1; Figure 4b,d). The effect of body mass, however, was modulated by environmental conditions. Low October degree days (around conception) and high ROS during gestation increased the negative effect of low body mass on the probability of reproductive success (Figure 4b,d). There was no strong evidence for a direct cost of reproduction on subsequent reproductive success ($\beta = -0.28 [-0.83, 0.12]$, Table S2), suggesting that the main mechanism for a reproductive cost of reproduction is through effects on body mass. The estimated cost of reproduction on mass was relatively constant through time, around -5.8 kg. However, the indirect effect of reproduction on subsequent reproduction was found to depend strongly on the previous body mass and environment. This is a consequence of the effect of previous mass on the mass cost of reproduction and the interactive effect of April mass and environment on reproductive success (Table 1; Figure 4b,d). The effects of environmental conditions and previous body mass ($w_{i,t-1}$) of the individuals were amplified by the nonlinear relationship between body mass and reproductive success (Figure 4b,d). For example, a 5.8 kg reduction in body mass will have less impact on reproductive success when representing a change from an expected body mass of 60 kg than from an expected body mass of 50 kg (Figure 4). Together, these relationships produce a strong association between environmental variables and the effect of the 5.8 kg body mass cost of reproduction on reproductive success. In years with benign environmental conditions, the estimated effect of the body mass cost of reproduction on expected subsequent reproductive success was $-10 [-18, -5]\%$, while the estimated

effect in harsh environmental conditions was $-49 [-60, -37]\%$ (Figure 4e). Overall, the reproductive cost of reproduction was highest in previously heavy individuals during harsh years (Figure S4).

3.3 | Determinants of survival

Survival was very high during prime age but lower for calves and older age classes (Table S1). Annual survival rate increased with April body mass (Table 1). In addition, there was a significant negative effect of ROS, independent of body mass (Table 1). The indirect survival cost of reproduction, through the body mass cost of reproduction, was weak. For a non-reproducing average 7-year-old female in an average environment, the body mass cost of reproduction resulted in a marginal decrease in expected annual survival from 97 [95.6, 98.3]% in non-reproducing individuals to 96 [94.3, 98.3]% in individuals that reproduced (Figure 5). The estimated survival cost of reproduction increased with ROS, with a 90.7 [82.8, 95.8]% versus 93.2 [87.5, 97.0]% survival probability for reproducing and non-reproducing females, respectively, in high ROS years (Figure 5).

4 | DISCUSSION

When partitioning the variation in net mass change, we found that extrinsic drivers had low impact on the costs of reproduction but high impact on non-reproductive mass change. We estimate the body mass cost of reproduction in Svalbard reindeer to be on average -5.8 kg, equivalent to approximately 11% of average adult body

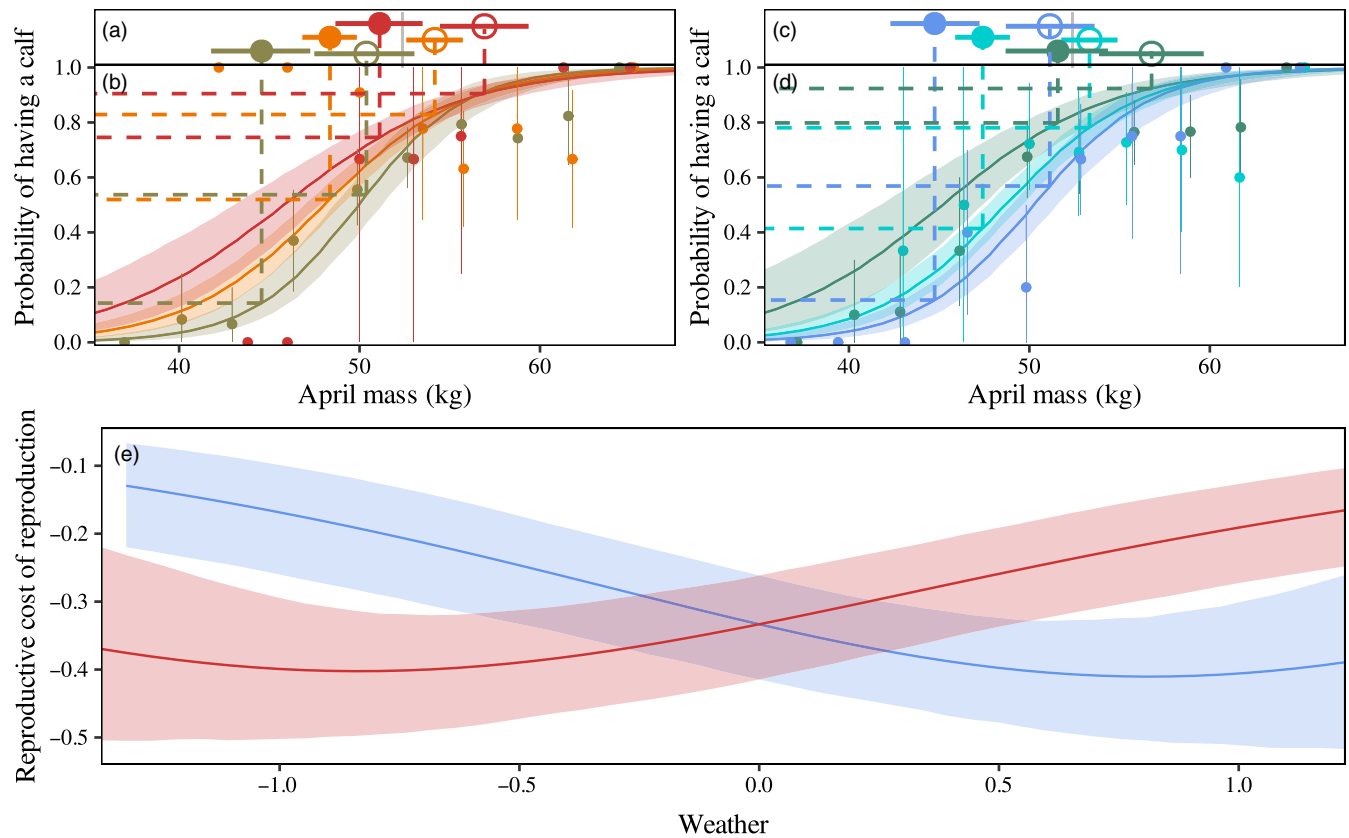


FIGURE 4 Effects of October degree days (a and b) rain-on-snow (ROS; c and d) on April body mass (a and c), and the relationship between the probability of having a calf next August and April mass (b and d) in female Svalbard reindeer between 1995 and 2019. In panels (a and c), the solid dots represent the expected mass in April (t) if a 7-year-old female of mean mass at time $t - 1$ (52.1 kg; vertical grey line) reproduced at time $t - 1$ while the open dots represent her mass in April (time t) if she did not reproduce at time $t - 1$. Red, orange and khaki lines and symbols show the outcome of a winter with high (90th percentile), average and low (10th percentile) October degree days, respectively. Blue, turquoise and green lines and symbols show the outcome of a winter with high (90th percentile), average and low (10th percentile) ROS, respectively. Panels (b and d) illustrate the posterior mean (and 95% CI) probability of having calf in August (at time t) as a function of April body mass, depending on the environment with points showing average reproductive success of prime-aged females grouped into body mass bins. Panel (e) illustrates how the reproductive cost of reproduction, in term of decrease in probability to have a calf, changes with the ROS (blue line and 95% CI) and October degree days (red line and 95% CI)

mass and higher than, for example, the 3% observed in bighorn sheep (Festa-Bianchet et al., 1998). The body mass cost of reproduction showed low temporal variability and was only weakly affected by environmental conditions. In contrast, overall mass change showed strong temporal variability and was under strong influence of extrinsic factors, with cold autumns and icy winters (high ROS) resulting in low or negative average mass change. Our study suggests that it was not variable body mass cost of reproduction that caused the high variation in reproductive cost of reproduction, but the highly stochastic environment that affected the ability of females to recover from the previous reproductive events observed in.

Supporting many previous studies, we found evidence for reproductive cost of reproduction to depend on environmental conditions (Barbraud & Weimerskirch, 2005; Bårdsen et al., 2008; Chambert et al., 2013; Creighton et al., 2009; Festa-Bianchet et al., 1998; Hamel, Côté, et al., 2010; Lourdais et al., 2002). However, the effect of environment on reproductive cost of reproduction in our study occurred despite a stable body mass cost of reproduction

(Figure 4). Our results suggest that in this capital breeder, the cost of reproduction on subsequent reproduction is context dependent because environmental conditions strongly affect a females' mass change and because of the nonlinear dependence of reproductive success on mass. In benign environments, females showed positive non-reproductive mass change, resulting in a high body mass, even when the cost of reproduction on mass was accounted for, and consequently, exhibited little cost of reproduction on subsequent reproduction. In contrast, when non-reproductive mass gain was low due to harsh environmental conditions, the cost of reproduction was likely to affect body mass in the steepest region of the body mass–reproductive success curve, leading to a large reduction in the probability of successful reproduction. This pattern was further amplified by an interaction effect between body mass and environmental variables affecting the slope of the reproductive success–body mass curve. The timing of peak allocation to a calf and investment in one's own body reserves are likely to also play a role in the evolution of these patterns (Fischer et al., 2011). Calves are mostly weaned

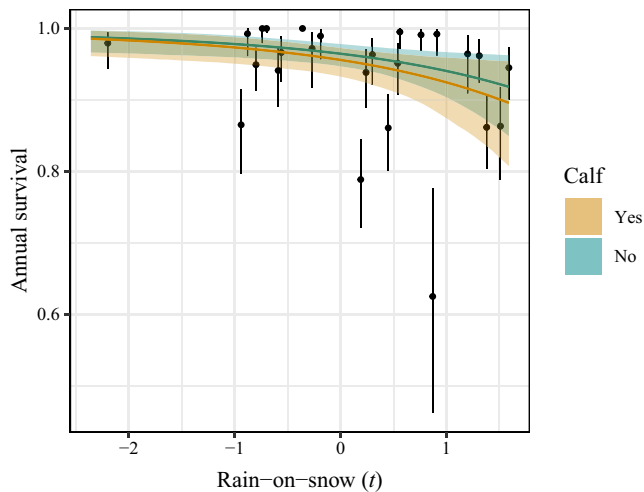


FIGURE 5 Indirect effects of rain-on-snow (ROS) on the annual probability of survival between August at time t and $t + 1$ of a 7-year-old average female reindeer given its reproductive success at time t (orange = had a calf, green = did not have a calf). Black points show annual estimates of survival from an unconstrained model

in September at a time when the two main environmental drivers impacting non-reproductive mass change (ROS and October day degrees) have yet to happen. While calf survival is high (mean = 80%), it is also highly variable from year to year (CV = 0.28, Bjørkvoll et al., 2016). The uncertain recovery of a female's own body condition by the end of peak resource availability in early August, in combination with the unpredictable survival of calves, has resulted in an energy allocation trade-off where the cost of reproduction on mass does not reduce future reproductive output, when winter conditions are good. When winters are bad, however, it affects future reproduction, but with virtually no survival cost. As such, our study supports the notion that reindeer are highly conservative in their reproductive strategy (Bårdsen et al., 2008; Bårdsen & Tveraa, 2012).

We found that the cost of reproduction on mass was marginally higher in high ROS winters. An increased cost of reproduction on mass in unfavourable environments has also been found in other species (Festa-Bianchet et al., 1998; Merilä & Hemborg, 2000; Trippel et al., 2014). This is in contrast to another capital breeder, the elephant seal *Mirounga leonina*, which was found to expend more energy on their pups under good condition (McMahon et al., 2017). Contrary to our expectation, environmental conditions during lactation (Clutton-Brock et al., 1989) were not associated with a cost of reproduction on mass, whereas the severity of winter (high ROS) was particularly marked. This suggests that in the Arctic, the relatively productive summers may be less constraining than the unproductive winters. Accordingly, Loe et al. (2019) suggested that antlers may be particularly important in competitive interactions for food in winter, and found that part of the cost of reproduction on mass acted through a reduction in antler size.

Also, we found significant but small effects of intrinsic factors, with the heaviest females losing 4 kg more mass following reproduction than the lightest ones (11% vs. 10% of body mass,

respectively). Similarly, lighter Weddell seals have been found to invest a lower proportion of body mass into offspring than heavy ones (Macdonald et al., 2020), which likely reflects a strategy to reduce the impact of reproductive success on future maternal body condition, subsequent reproductive success and survival. After accounting for differences in body mass, we found significant individual variation in the cost of reproduction on mass, suggesting that additional aspects of individual quality may play a substantial role in the costs of reproduction (Hamel et al., 2009; Moyes et al., 2011; Paterson et al., 2018), possibly associated with individual heterogeneity in resource acquisition (van Noordwijk & de Jong, 1986). Alternatively, some females may invest more in their offspring than others, suggesting inter-individual heterogeneity in life-history tactics in the population (Gangloff et al., 2018; Hamel et al., 2018). Such individual differences in reproductive strategy can be important causes of life-history and fitness variation (Oosthuizen et al., 2019). However, more studies would be needed to evaluate the impact of such heterogeneities on mother and offspring fitness. Among other things, it remains unknown whether the increased cost to mothers' fitness correlates with increased offspring survival.

As expected of a long-lived animal, survival of prime-aged female reindeer is high and shows little variation in time (Gaillard & Yoccoz, 2003) such that the cost of reproduction was more apparent on the next reproductive event than on subsequent survival (Hamel, Gaillard, et al., 2010). Indeed, we found no evidence of a direct cost of reproduction on survival and the indirect effect through April body mass was comparatively small. Furthermore, this effect was independent of the environment. Foregoing one reproductive event when resources are insufficient may not only prevent death, but will also allow a light individual to attain a higher mass by next April, even in harsh environment, increasing the likelihood of successful reproduction next year. Intermittent breeding is an efficient strategy to optimize fitness in many species (Baron et al., 2013; Bonnet et al., 2002; Desprez et al., 2018; Smout et al., 2020). While ovulation rates are consistently high in Svalbard reindeer, the probability of losing the calf is highly condition dependent (Albon et al., 2017). This may provide flexibility for reindeer to adjust energy allocation between reproduction and maintenance, depending on winter condition. Lifetime fitness consequences of this reproductive strategy, however, remain to be quantified.

Our novel state-space model enabled us to gain new insights into the costs of reproduction by partitioning the effects of environment on non-reproductive mass change from the direct effects on the cost of reproduction while accounting for missing observations. The model demonstrated that the cost of reproduction on mass was much more stable than non-reproductive mass change. The strong influence of the local environment on the cost of reproduction for subsequent reproductive success was primarily due to the combination of highly variable non-reproductive mass changes and a strong nonlinear dependence of reproductive success on body mass. In years with poor environmental conditions, the mass loss due to reproduction had a substantial impact on subsequent reproductive

success, while the impact was minor in years with good environmental conditions. Our results are consistent with the early theory of energy allocation (Williams, 1966), showing how the costs of reproduction are driven by interannual fluctuation in the body condition of individuals, resulting from the balance between reproductive and somatic investments.

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AUTHORS' CONTRIBUTIONS

A.S., S.A., L.E.L. and G.P. conceived the ideas and C.B., R.B. and G.P. developed the methodology; S.A., R.J.I., L.E.L., E.R., A.S. and V.V. collected the data over the last 25 years; G.P. analysed the data; G.P. and S.A. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

COMPETING INTERESTS

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

Data and code are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.80gb5mkrj> (Pigeon et al., 2021).

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