

# Silver spoon effects are constrained under extreme adult environmental conditions

GABRIEL PIGEON,<sup>1,8</sup> LEIF EGIL LOE,<sup>1</sup> RICHARD BISCHOF,<sup>1</sup> CHRISTOPHE BONENFANT,<sup>2</sup> MADRS FORCHHAMMER,<sup>3</sup>  
R. JUSTIN IRVINE,<sup>4</sup> ERIK ROPSTAD,<sup>5</sup> AUDUN STIEN,<sup>6</sup> VEBJØRN VEIBERG,<sup>7</sup> AND STEVE ALBON<sup>4</sup>

<sup>1</sup>Faculty of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås NO-1432 Norway

<sup>2</sup>Laboratoire de Biométrie et Biologie Évolutive, UMR CNRS 5558, Université de Lyon, Villeurbanne 69622 France

<sup>3</sup>The University Centre in Svalbard, Longyearbyen NO-9170 Norway

<sup>4</sup>The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH UK

<sup>5</sup>Faculty of Veterinary Science, Norwegian University of Life Sciences, P.O. Box 8146, Dep, Oslo NO-0033 Norway

<sup>6</sup>Department for Arctic Ecology, Norwegian Institute for Nature Research, Fram Centre, Tromsø NO-9296 Norway

<sup>7</sup>Norwegian Institute for Nature Research, P.O. Box 5685, Torgarden, Trondheim NO-7485 Norway

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**Abstract.** Early-life environmental conditions may generate cohort differences in individual fitness, subsequently affecting population growth rates. Three, nonmutually exclusive hypotheses predict the nature of these fitness differences: (1) silver spoon effects, where individuals born in good conditions perform better across the range of adult environments; (2) the “environmental saturation” hypothesis, where fitness differences only occur in intermediate adult environmental conditions; and (3) the “environmental matching” or “predictive adaptive response” (PAR) hypothesis, where fitness is highest when adult environmental conditions match those experienced in early life. We quantified the context-dependent effect of early-life environment on subsequent reproductive success, survival, and population growth rate ( $\lambda$ ) of Svalbard reindeer, and explored how well it was explained by the three hypotheses. We found that good early-life conditions increased reproductive success compared to poor early-life conditions, but only when experiencing intermediate adult environmental conditions. This is the first example of what appears to be both “beneficial” and “detrimental environmental saturation” in a natural system. Despite weak early-life effects on survival, cohorts experiencing good early-life conditions contributed to higher population growth rates, when simulating realistic variation in adult environmental conditions. Our results show how the combination of a highly variable environment and biological constraints on fitness components can suppress silver spoon effects at both extremes of the adult environmental gradient.

*Key words:* beneficial saturation; cohort; delayed environmental effect; detrimental saturation; environmental matching; fitness; predictive adaptive response; reindeer; silver spoon.

## INTRODUCTION

The environmental conditions experienced in early life can act directly on the developing phenotype (Gilbert 2001) and influence both the number of recruits and the recruits' subsequent fitness (Gaillard et al. 2003). Knowledge of how variation in early-life environmental conditions impact the fitness of wild animals is important for predicting the demographic consequences of environmental variation (Benton et al. 2001, Beckerman et al. 2002, Lindström and Kokko 2002), especially given that extreme variation appears to be increasing with current climate warming (Parmesan 2006). Understanding the source of individual heterogeneity in

survival and recruitment could be particularly relevant to the management of species that are harvested, in terms of setting quotas (Lindberg et al. 2013), or the conservation of populations that are small and at the edge of their species' range (Vindenes et al. 2008).

Where fitness components have been documented to vary between cohorts (individuals born in the same year, under the same environmental conditions), many studies have found a silver spoon effect at the individual level (sensu Grafen (1988); see Lindström (1999) for a review in birds and mammals, and Lummaa and Clutton-Brock (2002) for humans). Typically, phenotypes developing in good early-life conditions (with abundant resources) are physically larger, more fecund, and longer-lived, compared to those developing in poor early-life conditions (with scarce resources), irrespective of the adult environmental conditions (Fig. 1a).

Although silver spoon effects are often assumed to yield consistent fitness benefits, some studies suggest

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<sup>8</sup>E-mail: Gabriel.pigeon@nmbu.no

that the benefits of a good early life may depend upon the environmental conditions experienced later in life, because of associations with developmental plasticity (Gluckman et al. 2005, Monaghan 2008). In this context, the “environmental matching” hypothesis (also sometimes referred to as “predictive adaptive response”; Gluckman and Hanson 2004) proposes that early-life environmental conditions shape the phenotype to improve fitness when subsequently exposed to similar adult environmental conditions to those experienced in early life (Monaghan 2008). In this case, a phenotypes’ fitness is highest when the developmental and adult environmental conditions match (Fig. 1b). However, this model has been conceptually criticized (Wells 2007) and empirical support remains scarce (but see Beckerman et al. 2003).

The fitness advantages of a good early-life environment may also differ because most fitness measures are “bounded,” because of environmental and/or physiological constraints, which impose both upper and lower fitness limits. For example, species that give birth to only one young have a probability of reproduction bounded at zero and one. Given these bounded constraints, Engqvist and Reinhold (2016) proposed the “environmental saturation” model, which generates a sigmoidal shape in fitness across a range of adult environmental conditions. In good adult environmental conditions, all phenotypes attain high fitness (beneficial saturation), and in poor adult environmental conditions all phenotypes attain a low fitness (detrimental saturation). According to this model, differences in fitness between phenotypes will manifest themselves only in intermediate adult environmental conditions (Fig. 1c).

Species living in particularly variable environments, where density-independent (weather) factors often dominate impacts on reproduction and survival, are potentially promising case studies in which to address the fitness consequences of the interaction of early-life environmental conditions with variation in subsequent adult-life environmental conditions. For example, in both hot and cold deserts recent rapid climate warming, and the associated greater extremes in weather (IPCC 2014), can strongly affect the availability of resources for development and growth and lead to very low reproduction and/or offspring survival in some years (Garrott et al. 2012, Albon et al. 2017, Woodroffe et al. 2017). Previous work on Svalbard reindeer (*Rangifer tarandus platyrhynchus*) found that poor-quality early-life environmental conditions (ice-locked pastures during gestation) depressed cohort reproductive success, but only from the age of 7 yr onward (Douhard et al. 2016). That study did not detect cohort effects on projected population growth rates. However, the possibility of an interaction between the early-life environmental conditions and the subsequent adult environmental conditions was not considered explicitly.

In this paper, we investigate how cohort differences in fitness components of Svalbard reindeer are caused by early-life environmental conditions and modulated by variation in adult environmental conditions. Evidence supporting the silver spoon hypothesis (in its strict sense), would be expected to show that cohorts experiencing good early-life conditions have higher fitness components than cohorts experiencing poor early-life

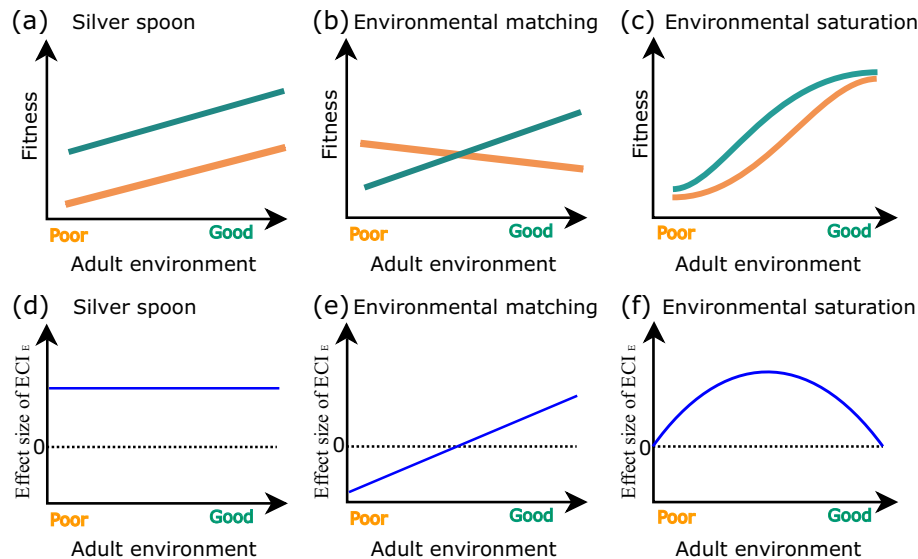


FIG. 1. Schematic representation of theoretical models for the fitness consequences of the early-life environmental conditions as a function of adult environmental conditions: (a) and (d) silver spoon; (b) and (e) environmental matching; (c) and (f) environmental saturation. Panels (a)–(c) show the effect on fitness on the response scale, whereas (d)–(f) show the expected effect size of early-life environmental condition ( $\beta ECI_E$ ) on the logit scale. Both (a) and (b) are adapted from Monaghan (2008), and (c) is adapted from Engqvist and Reinhold (2016). Orange lines represent cohorts born in a poor early-life environment and green lines represent cohorts born in a good early-life environment.

conditions, independently of the variation in subsequent adult environmental conditions (Fig. 1a). However, the expected improvement in fitness as adult environmental conditions improve could differ between cohorts experiencing a good early life vs. a poor early life, generating a statistical interaction between early life and adult environmental conditions (significantly different slopes). In contrast, evidence supporting the environmental matching theory must not only exhibit an interaction between early-life and adult environmental conditions, but predict that the fitness components of cohorts experiencing poor early life conditions would be higher than that of cohorts experiencing good early-life conditions when adult environmental conditions are poor. Monaghan (2008) suggested that this scenario might occur when developing under poor conditions gives rise to a small body size, which may be less costly than a large body size when food is in short supply, because of lower maintenance requirements, and hence be advantageous. Also, Monaghan (2008) argued that this was more plausible than the original conceptualization of the predictive adaptive response (Gluckman and Hanson 2004), where the fitness of cohorts experiencing poor early-life conditions would decline as the quality of the adult environment improves, whereas the fitness of the cohorts experiencing good early life conditions increases as the adult environmental conditions improve (Fig. 1b). Finally, evidence supporting the environmental saturation hypothesis would require an interaction between early-life environmental conditions and a quadratic effect of variation in the adult environment. This hypothesis specifically predicts that fitness differences between cohorts experiencing different early-life environmental conditions are only apparent when adult environmental conditions are intermediate. Cohort differences should shrink to zero when adult environmental conditions are either very poor, when very few individuals breed successfully, or very good, when all individuals breed successfully and survive, regardless of their early-life conditions (Fig. 1c).

Our overall objective is to distinguish between the three nonmutually exclusive hypotheses described, in order to understand how early-life environmental conditions interact with adult environmental conditions, and thereby generate differences in cohort fitness. To do so, we focus on two fitness components: (1) annual reproductive success (calf at heel) and (2) age-specific survival. In addition, we estimated the asymptotic population growth rate of individuals experiencing different early-life environmental conditions according to their adult environmental conditions. We used this as a proxy of fitness to evaluate demographic and evolutionary consequences of cohort effects.

## METHODS

### *Study area and reindeer population*

Our study area was located in Nordenskiöld Land, Svalbard (77°50'–78°20' N, 15°00'–17°30' E) and

consists of the main valleys Reindalen, Semmeldalen, and Colesdalen (Appendix S1: Fig. S1). Both the mean January daily temperature ( $-10.7^{\circ}\text{C}$ , SE = 5.1) and mean July daily temperature ( $6.7^{\circ}\text{C}$ , SE = 0.9) at Longyearbyen (<http://eklima.met.no>) increased significantly during the past two decades ( $0.44 \pm 0.16^{\circ}\text{C}$  per annum and  $0.073 \pm 0.027^{\circ}\text{C}$ , respectively (Albon et al. 2017)). Also, there was a tendency toward more rain-on-snow in later years (Albon et al. 2017). Although annual variation in population size is large, the population size has doubled in the past 20 yr and is currently estimated at around 1,800 females and calves. Annual declines in population size in this period has been caused mainly by rain-on-snow events, causing winter feeding sites to be ice-locked (see Albon et al. 2017 for more information).

### *Reindeer data*

Since 1995, wild female reindeer have been caught during late winter (mostly April), using a net stretched between snowmobiles (Omsjoe et al. 2009). At capture, all animals were weighed to the nearest 0.5 kg. New individuals were marked, mainly in their first year of life (10 months of age), using colored and numbered plastic ear tags and plastic collars (without VHF or GPS). Approximately 25% of the females present in the population were marked (Lee et al. 2015) and marked individuals were recaptured for up to 10 yr (mean number of captures per individual = 3.3).

In addition to late-winter captures, annual summer surveys were conducted to assess the presence or absence of a calf at heel and to assess survival of females. The summer survey was conducted on foot by two or more observers, using binoculars and telescopes, over a period of 10–14 d in late July/early August (except in 3 yr [1997–1999], when the period covered was approximately 8 weeks (earliest 24 June–latest 25 August)). In the open landscape, animals of all ages could be spotted and identified at long distances (more than 1 km). Because the observers moved in one direction through the study area and individual reindeer are quite stationary, very few are observed more than once in the same summer census. Carcasses of animals that died in the past winter could be spotted at a distance as a patch of white fur. Tags and collars normally stayed on the carcass enabling us to confirm death for a subsample of the marked individuals.

Reindeer may give birth for the first time when they are 2 yr old, but more commonly at 3 yr old. Calves are born in the first half of June and preweaning calf mortality typically occurs in the first days after birth (Albon et al. 2002); the presence of calf at heel later in the summer provided a good measure of reproductive success.

### *Quantifying environmental condition*

Several environmental variables, including rain-on-snow, autumn temperature, and population density can affect reindeer body mass and consequently fitness

(Albon et al. 2017). Because body mass reflects resource availability, and influences both reproduction and survival, mean annual age-specific body mass could be used as an integrative index to quantify the quality of the environmental condition in the year of birth.

Mean April mass of adult female Svalbard reindeer was highly variable from year to year (range = 40.3–57.1 kg; Albon et al. 2017). We excluded calves and yearlings because their lower survival rate, which is a function of their smaller body mass, is likely to bias the estimates because of nonrandom missing fractions (Nakagawa and Freckleton 2008). In addition, to account for potential bias due to annual changes in the age structure and capture date on the average annual body mass, we estimated April body mass of adult females using a linear mixed model. The model was fitted with no intercept and the effects of year modeled as a factor. Age was also modeled as a factor (2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16) without any grouping into age classes, using 8-yr-olds (prime aged) as a reference. We used one level per year of age to reflect age-specific growth and account for decrease in mass of older individuals. Capture date was modeled as a continuous variable (using mean capture date [18 April] as a reference date). The model also included the individual identity as a random effect, because individuals were repeatedly caught and weighed throughout their lives.

As our Environmental Condition Index (ECI), we used the estimated effects of year from our April mass model (giving us the predicted mean body mass of 8-yr-olds at mean capture date). This variable was scaled to a mean of 0 and a standard deviation of 1 and considered as our continuous measure of a given year's environmental condition. This ECI reflected, in part, the presence of rain-on-snow events (Pearson's  $r = -0.69$ ), but was a significantly better predictor of reproductive success ( $\Delta AIC_c = 34.7$ ). For easier interpretation, we also explored a categorical version of this measure of environmental conditions (lower third, intermediate third, and upper third, Gelman and Park 2008), where years with values  $< -0.65$  were regarded as poor years, years with values in the range  $[-0.65, 0.3]$  were regarded as intermediate, and years with values  $> 0.3$  were regarded as good in terms of environmental condition.

#### *Cohort variation in annual reproductive success*

Successful reproduction was considered to have occurred when a female was seen with a calf at heel during the summer census. The binary response was analyzed using generalized additive mixed models in the `gamm4` package in R (Wood and Scheipl 2017) with a binomial error distribution and a logit link function. This modeling approach was chosen because it allows nonlinear patterns in the data to be modeled by smoothing splines, which gave a good fit to the age-specific values. We restricted the analysis of reproductive success to cohorts born between 1995 and 2015, because our ECI

was only quantified from 1995 onward. Overall, this resulted in 1,362 reproductive events from 369 individuals belonging to 21 cohorts. Our starting baseline model (Table 1, Model 0) included age fitted as a smoothing spline (with a basis dimension = 10) and the  $ECI_A$  (the measure of environmental condition experienced each year as an adult) fitted as a linear fixed effect. Female identity, year, and cohort were fitted as random intercepts in the model. We then included the effect of early-life environmental conditions ( $ECI_E$ ) as a fixed effect to this baseline model to test for the presence of a silver spoon effect (Fig. 1d, Table 1, Model 1). Next, we added the interaction between early-life and adult environmental conditions (Table 1, Model 2), which is necessary for both environmental matching and environmental saturation hypothesis. To account for the presence of a smaller effect of early-life environmental conditions when adult environmental conditions were either good or poor (environmental saturation), than when adult environmental conditions were of intermediate quality, we also added the interaction between early-life environmental conditions ( $ECI_E$ ) and a quadratic effect of adult environmental conditions (Fig. 1f, Table 1, Model 3). A stronger effect of  $ECI_E$  at intermediate  $ECI_A$  would result in a significant effect of both the main effect of  $ECI_E$  and a significant negative effect of its interaction with the quadratic term,  $ECI_A^2$ . Corrected Akaike information criterion ( $AIC_c$ ) of all models is provided in the supplementary material (Table 1).

#### *Cohort variation in annual survival*

Because annual sighting probability is imperfect (mean = 49%), survival was analyzed using a capture-mark-recapture (CMR) model implemented in JAGS (Plummer 2010) and fitted through R using Rjags (Plummer 2016), because of the imperfect detection of individuals (Lebreton et al. 1992). We ran three chains of 11,000 iterations each, with a burn-in of 1,000, thinning by 10. Convergence was assessed visually and using the Gelman and Rubin convergence diagnostic (Gelman and Rubin 1992). The likelihood of the mark-recapture data were constructed using a state-space formulation of the Cormack–Jolly–Seber model, similar in specification to the model used by Lee et al. (2015). Sighting probability was allowed to vary between years and census seasons following a normal distribution on the logit scale (Lee et al. 2015). Survival  $s$  of individual  $i$  was allowed to vary with time (across year and season)  $t$ , such that  $\text{logit}(s_{i,t}) = \beta X_{i,t} + \varepsilon_t$ , where  $X$  is the design matrix of the predictive variables ( $ECI_E$  and  $ECI_A$ ),  $\beta$  the associated vector of regression coefficients including the effect of age, and  $\varepsilon_t$  is a random intercept for year (see Data S1 for JAGS code). Like Lee et al. (2015), we modeled age using age classes: 0, 1, 2, 3–8, 9–11, and 12+ yr old. Following the approach we used for analyzing reproduction, we then sequentially

TABLE 1. Parameter estimates (with 95% confidence intervals in parentheses) for the model looking at the varying effects of early-life ( $ECI_E$ ) and adult environmental conditions ( $ECI_A$ ) on (A) reproductive success and (B) survival. The models included effects of both  $ECI_E$  and  $ECI_A$ , the interaction between the two, and the interaction between  $ECI_E$  and the quadratic  $ECI_A$ . Both  $ECI_A$  and  $ECI_E$  were treated as continuous variables. All models included age, fitted as a nonparametric spline (for reproductive success) or age classes (for survival). Terms associated with significant effects are in boldface.

Parameter	Model 0	Model 1	Model 2	Model 3
<b>(A)</b>				
$ECI_A$	<b>0.919 (0.739; 1.100)</b>	<b>0.926 (0.743; 1.109)</b>	<b>0.938 (0.750; 1.125)</b>	<b>0.884 (0.696; 1.072)</b>
$ECI_E$		0.159 (−0.020; 0.338)	0.168 (−0.010; 0.346)	<b>0.310 (0.099; 0.520)</b>
$ECI_E:ECI_A$			−0.062 (−0.261; 0.137)	−0.148 (−0.361; 0.066)
$ECI_A^2$				−0.112 (−0.254; 0.030)
$ECI_E:ECI_A^2$				<b>−0.182 (−0.342; −0.022)</b>
AIC	1,577.5	1,576.9	1,578.5	<b>1,573.8</b>
Delta AIC	3.7	3.1	4.7	<b>0</b>
<b>(B)</b>				
$ECI_A$	0.224 (−0.076; 0.556)	0.217 (−0.101; 0.547)	0.220 (−0.093; 0.554)	0.078 (−0.313; 0.507)
$ECI_E$		<b>0.132 (0.001; 0.262)</b>	<b>0.139 (0.013; 0.266)</b>	0.172 (−0.008; 0.342)
$ECI_E:ECI_A$			0.076 (−0.086; 0.236)	0.028 (−0.192; 0.235)
$ECI_A^2$				−0.136 (−0.365; 0.102)
$ECI_E:ECI_A^2$				−0.037 (−0.173; 0.102)
WAIC	<b>11,449.7</b>	11,459.7	11,452.1	11,454.3
Delta WAIC	<b>0</b>	10.0	2.4	4.6

included the effects of adult environment ( $ECI_A$ ), early environment ( $ECI_E$ ), their interaction ( $ECI_E:ECI_A$ ), and the nonlinear interaction ( $ECI_E:ECI_A^2$ ) and compared the models using deviance information criterion (Spiegelhalter et al. 2002). The effects of  $ECI_E$ ,  $ECI_A$ , and their interactions were modeled to affect survival only for individuals 2 yr old or older. In all models, the effect of environment on survival of individuals <2 yr of age was modeled as only being dependent on the environment in the current year to avoid short-term effects of environment being confounded with the long-term effects of early life. To make the most of the available information when estimating CMR parameters, such as age-specific survival and annual sighting probability, we included also marked individuals with known age born before 1995 in the survival analyses. For these individuals ( $n = 109$  out of the total 707 individuals),  $ECI_E$  could not be calculated. To obtain an estimate of  $ECI_E$  in these early years, we modeled the relationship between ECI and rain-on-snow events using linear regression (Pearson's  $r = -0.53$ ) and used the posterior predictive distribution from this model to estimate the  $ECI_E$  for years before 1995.

#### Cohort variation in lifetime fitness

In order to quantify the potential lifetime fitness consequences of  $ECI_E$  (Fisher 1930), we built Leslie matrix models (Caswell 2001) for each combination of poor, intermediate, and good  $ECI_E$  and  $ECI_A$ , assuming a constant  $ECI_A$  during adulthood. We entered the age-specific values of reproductive success and survival predicted by the full model (Model 3), with their uncertainty (drawn 3,000 times from a normal distribution

with standard deviation equal to the predicted value's SE for reproduction or based on the posterior distributions for survival), into the matrix models and computed the posterior distribution of asymptotic growth rate (hereafter denoted as  $\lambda$ ) of each of these groups as a measure of ECI-specific fitness (Dohard et al. 2014). Given that we were only interested in long-term effects, we did not consider in this analysis the effect of current adult environment or the uncertainty in the survival of calves. In addition, we estimated the stochastic population growth rate for each combination of poor, intermediate, and good  $ECI_E$ , and stochastic  $ECI_A$  based on the observed variation in  $ECI_A$  to see if we would expect fitness differences between cohorts in a more realistic environment. To do so, we generated a Leslie matrix for each of the observed  $ECI_A$  given a certain  $ECI_E$  using the previously described approach. We then used the stochastic growth rate function from the popbio package (Stubben and Milligan 2007), in R, to calculate the stochastic population growth rate based on these matrices. We repeated this procedure 3,000 times in order to get estimates of uncertainty around the predicted stochastic population growth rate.

#### RESULTS

The age-specific (8-yr-old) probability of having a calf at heel, our measure of reproductive success, varied between years from 0.09 to 0.81 (mean = 0.565; SD = 0.213), and annual survival for an 8-yr-old varied between years from 0.89 to 0.98 (mean = 0.953; SD = 0.02). Mean annual reproductive success increased as adult environmental conditions improved (Table 1A), but this was not the case for survival (Table 1B).

The effects of early-life conditions on cohort reproductive success were modulated by variation in adult environmental conditions in a way that supported the environmental saturation model (Fig. 2). The interaction between the  $ECI_E$  and the quadratic effect of  $ECI_A$  was significant and negative ( $P = 0.026$ , Table 1). Differences between cohorts born under different early-life environmental conditions were only significant in intermediate adult environmental conditions, and the biggest differences were found when  $ECI_A$  was  $-0.4$  (Fig. 3). In average adult environments, cohorts born in poor years had a lower probability of having a calf at heel (0.45, 95% CI = 0.34–0.58 for 8-yr-olds) compared to those born in good years (0.63, 95% CI = 0.54–0.71); a difference between poor and good cohorts of  $-0.17$  (95% CI =  $-0.31$  to  $-0.02$ ). Although Fig. 2 suggests that the opposite occurred when adult environment was either very good or very poor, cohorts experiencing poor early-life conditions tended to have slightly higher probability of having a calf at heel; these differences between cohorts were not significant (differences when adult environment was very good: 0.13, 95% CI =  $-0.06$  to 0.29, when very poor: 0.07, 95% CI =  $-0.06$  to 0.32). Alternative models considering both early-life and adult environmental conditions as categorical variables, and hence not dependent on the distribution of ECI data points and curve fitting through them, led to similar conclusions (Appendix S1: Tables S2 and S3, Fig. S2a). In addition, the prediction of environmental matching was not met. Cohorts from poor early-life environment never had significantly higher reproduction than good cohorts, nor was the interaction of early-life environment strong enough to generate an opposite response to adult environment (Figs. 2 and 3).

Neither the simple silver spoon nor environmental matching hypotheses (Models 1 and 2) were supported by our analysis of reproductive success. Both these models failed to detect a significant additive effect of early-life environmental conditions ( $ECI_E$ ) on reproduction (Table 1A). Furthermore, the simple interaction with the adult environmental conditions ( $ECI_E:ECI_A$ ), a specific prediction of the environmental matching hypothesis, was not significant (Table 1A, Model 2).

As shown previously (Lee et al. 2015, Albon et al. 2017), survival of adult female reindeer was high (survival of 8-yr-old = 0.978, CI = 0.970–0.986; Appendix S1: Figs. S2b, S4), and had a tendency to be positively related to the  $ECI_A$  (Table 1B, Model 0):  $\beta = 0.224$ , 95% CI =  $-0.076$ –0.556;  $\beta$  young = 0.632, 95% CI = 0.278–0.987). Model selection using WAIC (Table 1B) suggested no improvement in the models after adding early-life environment ( $ECI_E$ ) or the interactions between early-life environmental conditions and adult environmental conditions. This was probably because the coefficients in the models tended to be small, and often the confidence intervals overlapped zero. However, when exploring the silver spoon hypothesis there was a marginally significant additive effect of  $ECI_E$  (0.132, 95%, CI = 0.001–0.262) on survival, but this tended to reduce the effect of the adult environmental conditions slightly (Table 1B, Model 1). There was no support for either the environmental matching hypothesis nor for the environmental saturation hypothesis in the absence of a significant simple interaction between early-life and adult environmental conditions (Table 1B, Model 2 and 3). Alternative models considering both early-life and adult environmental conditions as categorical variables and their interaction lead to similar conclusions (Appendix S1: Tables S3 and S4, Fig. S2b). Thus, in the

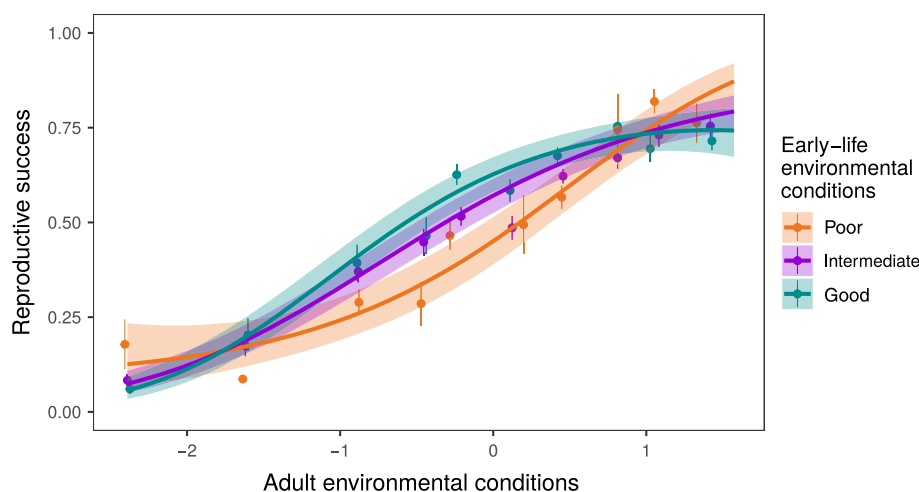


FIG. 2. The effect of early-life environmental conditions on reproductive success, measured as the probability of having a calf at heel for an 8-yr-old female Svalbard reindeer, depending on adult environmental conditions. Bold-colored lines show predictions from Model 3 (Table 1A); their SEs are represented by corresponding lighter colors. Predictions were made for cohorts experiencing three levels of early-life environment: poor (orange; 5th percentile), intermediate (purple), and good (green; 95th percentile). Points show observed average reproductive success, corrected for age within 10 percentile bins of adult environment quality.

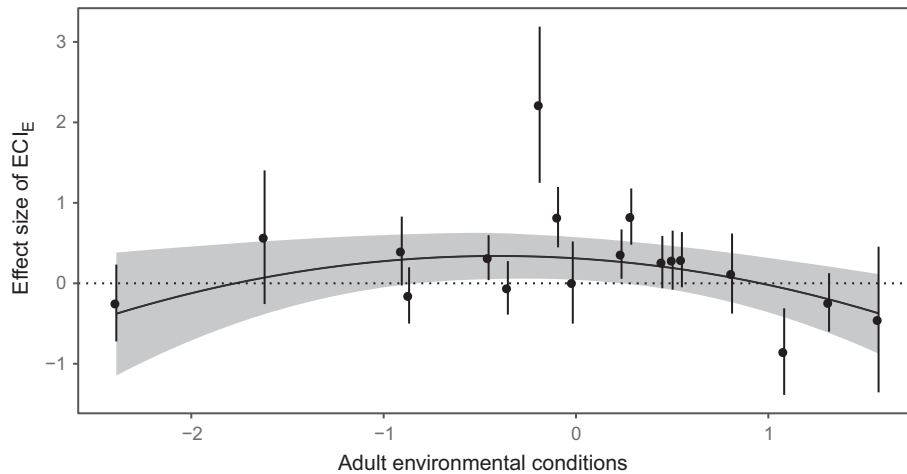


FIG. 3. Effect size, on the logit scale, of early-life environmental conditions ( $ECI_E$ ) on the probability of having a calf at heel as a function of adult environmental conditions ( $ECI_A$ ). The shaded region represents the 95% confidence interval. The points show estimated effect of  $ECI_E$  on the probability of having a calf at heel for each year of the study along with SE. Yearly effect estimates were obtained from a GAMM model with ID and cohort as random intercept, age fitted as a nonparametric smoothing spline, and year (as a factor) and its interaction with  $ECI_E$  fitted as parametric fixed effects (Appendix S1: Fig. S3). One-year-olds and cohorts with too few events were removed from analysis to allow convergence.

case of adult survival, we found no support for silver spoon effect and no support for environmental matching or environmental saturation.

For the lifetime fitness measure ( $\lambda$ ), we detected no significant effect of early-life environmental conditions when adult environmental conditions were good. The strongest difference between cohorts was found in intermediate adult environmental conditions, where  $\lambda$  was significantly lower in cohorts born in poor compared to good early-life environmental conditions (Fig. 4). Under poor adult environmental conditions, cohorts experiencing poor early-life environmental conditions had a slightly higher  $\lambda$  than those experiencing good early-life environmental conditions. When estimating stochastic population growth rate to reflect natural variation in adult environmental conditions, we found significantly different values of  $\lambda$  between cohorts experiencing poor early-life environmental conditions ( $\lambda = 1.056$ , CI = 1.037–1.073) and good early-life environmental conditions ( $\lambda = 1.094$ , CI = 1.078–1.108), with those from intermediate early-life environment in between ( $\lambda = 1.081$ , CI = 1.066–1.095; Fig. 4).

## DISCUSSION

The hypothesis of environmental saturation predicts that differences in fitness between cohorts experiencing contrasting early-life environments manifest themselves under intermediate, rather than under either poor or good adult environmental conditions (Engqvist and Reinhold 2016). Our study is the first example of both beneficial and detrimental environmental saturation in a natural system, where the silver spoon benefits dissipated when environmental conditions were very good or

very poor. Only when adult environmental conditions were intermediate did we find significant differences in the probability of a calf at heel in cohorts experiencing contrasting early-life environments. This suggests that for species with biological constraints on fitness components living in highly variable environments, suppression of silver spoon cohort effects can occur at both extremes of the adult environmental gradient.

Unlike reproductive success, there was a negligible effect of early-life environmental conditions on adult survival, as variation in survival was primarily related to adult environmental conditions. The overall much weaker cohort effects on survival as well as the absence of evidence for significant interactions between the effects of early-life and adult environmental conditions may be explained by the high demographic importance of adult survival for long-lived species, which is therefore strongly canalized against temporal variability (Gaillard et al. 2000, Gaillard and Yoccoz 2003). Alternatively, viability selection before calves are marked could make the detection of long-term effects of poor early-life conditions difficult by removing low-quality individuals prior to our initial capture at 10 months of age. Given the strong influence of early-life environmental conditions on reproductive traits, we found a significant difference in population growth rate (i.e., cohort-specific  $\lambda$ ) between cohorts experiencing different early-life environmental conditions, unlike the findings of previous studies that ignored the complex interactions between current and early-life environment (Douhard et al. 2016). This difference in population growth rate was significant in both an invariable intermediate environment and a more representative, stochastic adult environment.

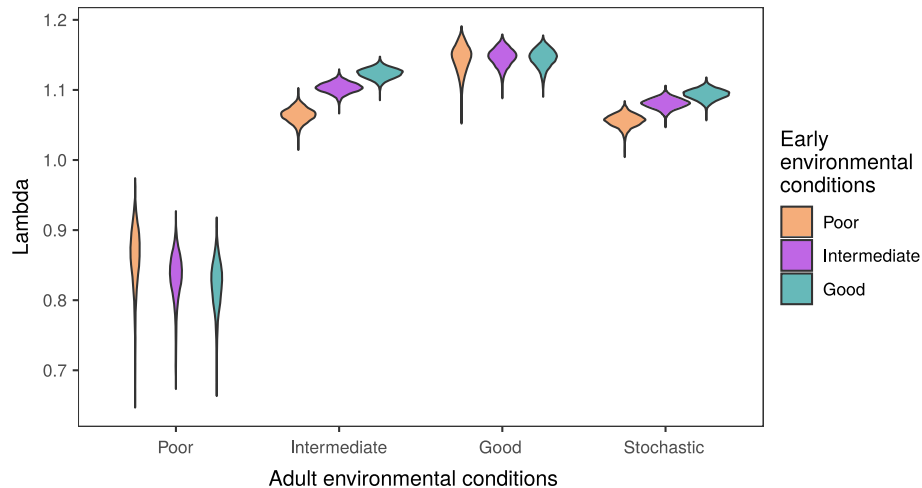


FIG. 4. Posterior distributions of estimated population growth rate ( $\lambda$ ) for cohorts born under poor (5th percentile), intermediate (mean), and good (95th percentile) early-life environmental conditions and experiencing different adult environmental conditions.

Environmental saturation may be most common in systems with highly variable environmental conditions between years, and in species with constraints on their maximum reproductive output. In such systems, the lower end of the distribution of environmental conditions may reflect conditions that are so unfavorable that all animals do poorly, independent of their individual quality. At the upper end of the distribution, there may be no limiting effect of environmental conditions on any cohorts/phenotypes, and intrinsic biological constraints may become the limiting factor. The Arctic tundra is a biome that experiences highly variable environmental conditions. Accordingly, many Arctic birds and mammals exhibit particularly large variation in reproduction between years; for example, geese (*Chen caerulescens atlantica*; Reed et al. 2003, Morrisette et al. 2010) wader species (Meltofte et al. 2007) and caribou/reindeer (Larter and Nagy 2000). In poor years, even reindeer cohorts that have experienced good early-life environmental conditions are starving and lose body mass, so that they end the winter no heavier than cohorts that had experienced poor early-life environments (*unpublished results*). In contrast, when the overall adult environmental conditions are very good, we see beneficial saturation, as reproductive success is predominantly limited by the innate constraint of only one calf per female in reindeer. Even though cohorts that experienced poor early-life environmental conditions are about 5 kg lighter at the end of winter than cohorts that experienced good early-life environmental conditions (*unpublished results*), they have the reserves necessary to rear their single calves. This is supported by the observation that nearly all adult females have a calf at heel after favorable winters (Veiberg et al. 2017). Given that climate variability is expected to increase in the future (Diefenbaugh et al. 2017, Bathiany et al. 2018), cases of environmental saturation on fitness differences

associated with early-life environments may become increasingly common worldwide.

Few studies have investigated the potential interactions between early-life environmental conditions and adult environmental conditions to allow conclusions to be made regarding the relative likelihood of environmental matching, environmental saturation, and the silver spoon effect. Nonetheless, those studies that have explicitly explored this interaction suggest that environmental matching is rather rare (Beckerman et al. 2003, but see Douhard et al. 2014), whereas the silver spoon effect is relatively common (Descamps et al. 2008, Pigeon and Pelletier 2018), particularly for measures of reproductive success. One reason for the lack of examples of environmental saturation may be methodological. We are not aware of previous attempts to model the interaction between early-life environmental conditions and the adult environmental conditions using a polynomial function, rather than solely linear terms. Indeed, simpler models were unable to detect significant effect of early-life environmental conditions on reproduction in any adult conditions (Model 1, Table 1A). Also, it should be noted that environmental matching, environmental saturation, and the silver spoon effect are not mutually exclusive hypotheses for the relationship between fitness and environmental quality. Indeed, Monaghan (2008) suggested that early-life differences between cohorts might lead to some phenotypes displaying silver spoon effects and others exhibiting environmental matching. Our observations from Svalbard reindeer is a case in point. Although consistent with environmental saturation at both extremes of adult environmental conditions, the differences between cohorts were consistent with a silver spoon effect when the conditions were intermediate. Similarly, a study of bighorn sheep (*Ovis canadensis*) found evidence of beneficial saturation in low-density conditions but silver spoon effects in high-density conditions (Pigeon et al. 2017).



## CONCLUSIONS

Variation in resource availability in early life can cause long-lasting cohort effects. In this study, we show that differences in environmental conditions experienced during early life cause contrasting patterns in fitness when individuals are exposed to environmental variation as adults. Our study provides clear empirical evidence that the concept of a purely additive effect of early-life environment, the silver spoon effect, may represent an oversimplification. Ignoring the complexity of long-term effects of early-life environment will hinder our capacity to detect them. Furthermore, as environmental conditions are becoming more variable, systems showing environmental saturation may become more apparent.

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