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The influence of weather conditions during gestation on life histories in a wild Arctic ungulate

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1 **The influence of weather conditions during gestation on life histories in a wild**

2 **Arctic ungulate**

3

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Abstract

The internal predictive adaptive response (internal PAR) hypothesis predicts that individuals born in poor conditions should start to reproduce earlier if they are likely to have reduced performance in later life. However whether this is the case remains unexplored in wild populations. Here, we use longitudinal data from a long-term study of Svalbard reindeer to examine age-related changes in adult female life-history responses to environmental conditions experienced *in utero* as indexed by rain-on-snow (ROS_{utero}). We show that females experiencing high ROS_{utero} had reduced reproductive success only from 7 years of age, independent of early reproduction. These individuals were able to maintain the same annual reproductive success between 2 and 6 years as phenotypically superior conspecifics that experienced low ROS_{utero} . Young females born after high ROS_{utero} engage in reproductive events at lower body mass (about 2.5 kg less) than those born after low ROS_{utero} . The mean fitness of females that experienced poor environmental conditions in early life was comparable to that of females exposed to good environmental conditions in early life. These results are consistent with the idea of internal PAR and suggest that the life-history responses to early-life conditions can buffer the delayed effects of weather on population dynamics.

Key words: climate change, cohort, development, predictive adaptive response, phenotypic plasticity, Svalbard reindeer.

41 **1. Introduction**

42 There is now overwhelming evidence that ‘early life’ represents a sensitive window influencing
43 the phenotype in various species [1, 2]. Environmental conditions prevailing during this period,
44 when the architecture of the body is being established [3], often show short-term effects, for
45 instance by influencing juvenile survival [4]. Conditions early in life can also have long-lasting
46 effects on adult phenotypes, from physiology and metabolism [5], to life-history traits such as
47 body growth, reproduction and survival [6-8]. Early-life conditions can thus influence life-
48 history trajectories of entire cohorts (set of individuals born within the same birth pulse). Such
49 ‘delayed cohort quality effects’ (sensu [9]) can affect population dynamics [10, 11]. Less well
50 understood is how individuals respond to these long-term, environmentally induced changes.
51 Studies have typically considered that an adverse early environment imposes severe constraints
52 on development, resulting in stunted, poorly performing individuals (silver spoon effect) [12,
53 13]. There is an emerging view, however, that individuals can mitigate the effects of poor early-
54 life conditions with adaptive changes in behavior, morphology or reproduction [14, 15], but
55 supporting data are still scarce [16, 17].

56 The internal predictive adaptive response (internal PAR, [15]) hypothesis was recently
57 developed to account for observed associations between poor early-life conditions and
58 acceleration of reproductive timing in humans. Nettle and colleagues proposed that “*early-life*
59 *adversity has a lasting negative impact on the individual’s somatic state, such that her health is*
60 *likely to fail more rapidly as she gets older, and there is an advantage to adjusting her*
61 *reproductive schedule accordingly*” [15]. More generally, individuals born under poor conditions
62 should start to reproduce earlier if they are likely to have reduced performance (survival and/or
63 reproductive success) in later life or faster rates of senescence compared with individuals born
64 in better conditions. The internal PAR differs from the external PAR, which is a form of
65 developmental plasticity where individuals anticipate their adult environment and adjust their
66 physiology accordingly [18]. In the internal PAR, what individuals are ‘predicting’ from their
67 early environment is not the state of their future environment but rather the future state of their
68 own body [15]. The internal PAR hypothesis appears more relevant than the external PAR in
69 long-lived species living under variable environments, where the assumption that the
70 environment in early life provides a reliable clue of the environmental conditions during

71 adulthood is unlikely [19, 20]. However, while tests of the external PAR hypothesis in long-lived
72 species have repeatedly led to its rejection (see [21] in roe deer, [22] in baboon, [23] in
73 preindustrial humans), direct tests of the internal PAR hypothesis are currently lacking in wild
74 populations.

75 An increasing number of studies have shown that poor environmental conditions in early
76 life can result in either accelerated senescence or reduced reproductive success and survival at
77 old ages [24-30], but the pathways leading to these patterns are poorly understood. There are at
78 least two mechanisms through which such relationships could occur. First, poor early-life
79 conditions may directly affect physiological functions, such as antioxidant defenses and telomere
80 dynamics whose negative consequences on performance often do not manifest themselves until
81 later in life [31]. Second, individuals born in poor environmental conditions may suffer from
82 increased costs of reproduction during early adulthood [26]. The disposable soma theory predicts
83 that increased reproductive effort during early adulthood should be accompanied by reductions in
84 late-life performance [32, 33]. However, costs of reproduction can only be evident among low-
85 quality individuals that consistently acquire less resources than high-quality individuals [34].
86 Because the internal PAR assumes that reduced performance in later life associated with poor
87 early-life conditions results from direct effects of environment rather than increased costs of
88 early reproduction, disentangling these two mechanisms of long-lasting effects of early
89 environment is important.

90 In this paper, we take advantage of a long-term study of female Svalbard reindeer
91 (*Rangifer tarandus platyrhynchus*) to evaluate the support for the internal PAR hypothesis.
92 Living at high latitudes, Svalbard reindeer experience considerable variation in winter resource
93 availability [35], particularly due to variation in rain-on-snow (ROS) events which create ice
94 layers on the ground or in the snow pack [36], and limit access to vegetation in winter [37]. We
95 focus our analysis on ROS events *in utero* (ROS_{utero}) because females that experienced high
96 ROS_{utero} were lighter and smaller during both the juvenile and adult stages than females
97 experiencing low ROS_{utero} (figure 1).

98 We begin by testing the assumptions of the internal PAR hypothesis. We investigate
99 whether females experiencing high ROS_{utero} show steeper rates of reproductive and actuarial
100 senescence or reduced performance in late life compared with females born under more
101 favorable conditions to low ROS_{utero}. We evaluate whether these differences result from

102 differential costs of early reproduction. We also examine the effects of ROS_{utero} on reproductive
103 success and survival during early adulthood to determine if individuals born in poor conditions
104 are at a permanent disadvantage, as predicted by the silver spoon hypothesis.

105 The internal PAR predicts an early onset of reproduction for individuals born under poor
106 conditions. However, this does not take into account biological constraints on age at first
107 reproduction. In large mammalian herbivores such as Svalbard reindeer, young females must
108 reach a threshold body mass to ovulate (see [38] for a review). Information on age at first
109 reproduction is unavailable for most female reindeer because we did not capture them every year,
110 but there is good quality data available on pregnancy rate and mass. Therefore, we focus on how
111 the mass-specific probability of pregnancy for young females varies with ROS_{utero} . We test the
112 prediction derived from the internal PAR hypothesis that young females born after high ROS_{utero}
113 should achieve a 50% probability of pregnancy at a lower body mass compared to females born
114 after low ROS_{utero} . Finally, we compare mean fitness of females born after high vs. low ROS_{utero} .
115 The silver spoon hypothesis predicts that individuals experiencing good environmental
116 conditions during early life should have greater fitness than individuals facing poor
117 environmental conditions, whereas no fitness differences should be detected according to the
118 internal PAR.

119

120 **2. Materials and Methods**

121

122 **(a) Svalbard reindeer as a biological model**

123

124 The Svalbard reindeer is a subspecies of *Rangifer tarandus* endemic to the Arctic archipelago of
125 Svalbard. It represents one of the northernmost populations of *Rangifer* and is highly sedentary
126 with no migration [39]. Maximum documented longevity is 17 years in females and 12 years in
127 males [40]. The mating system is polygynous with the main rutting activity peaking in early
128 October, and a subsequent highly synchronized birth period in early June [41]. Females are
129 iteroparous and can give birth to a single calf each year from 2 years of age onwards. There are
130 no large terrestrial predators for reindeer in Svalbard and human harvesting of reindeer is limited.

131

132 **(b) Weather data**

133
134 The weather data were collected at Longyearbyen airport (77°54'N, 16°48'E) by the Norwegian
135 Meteorological Institute. We calculated ROS as the amount of precipitation that fell at
136 temperatures above one degree C, between 1 November and 30 April when females were
137 currently gestating [42]. We did not detect any evidence of temporal autocorrelation in ROS
138 (electronic supplementary material, figure S1). In all models, we entered ROS_{utero} as a two-level
139 factor separating high ROS_{utero} (≥ 10 mm) from low ROS_{utero} (< 10 mm). The threshold of 10
140 mm, determined from the distribution of ROS that shows a clear grouping (electronic
141 supplementary material, figure S2), has previously been used for investigating the effects of
142 heavy ROS on Svalbard reindeer population growth rates [43].

143

144 (c) Study area and population

145

146 The study was carried out in Nordenskiöld Land, Spitsbergen (77°50'-78°10'N, 15°00'-
147 17°00'E). The population has been monitored by capture-mark-recapture since 1994. A small
148 number of females were captured in August 1994 using chemical immobilization but since 1995,
149 female have been caught using a net attached to two handheld poles between snow-scooters in
150 the winter (mostly in April/early May) [44]. Annual population size estimates (all female adults
151 plus calves of both sexes) ranged between 733 in 1996 and 1758 in 2014 [45]. All females
152 included in this study were of known age, because they have been marked as calves at 10-11
153 months or yearlings at 22-23 months, when age can be reliably established on the basis of size
154 and tooth eruption [46]. Approximately 25% of the females present in the population were
155 marked [44]. Although this study is based on individual-based longitudinal data, not all females
156 were captured every year with an estimated annual recapture probability ranging between 0.25
157 and 0.68 [47]. When age is referred to in this study, it corresponds to the individual age in June,
158 1-2 months after capture and around the normal timing of birth. Animals captured at the age of 1
159 year and 10 months are therefore referred to as 2 year olds, etc. As we are interested in long-
160 lasting effects of environmental conditions in early life, we restricted the latest cohort in our
161 sample to females born in 2010, yielding a total of 18 cohorts, born from 1993 to 2010. Our last
162 year of data was 2013 and 2014 for reproduction and survival analyses, respectively.

163 At capture, body mass was measured to the nearest 0.5 kg and pregnancy status was

164 determined from the progesterone concentration in blood samples and ultrasound diagnosis [48].
165 In addition to the winter captures, annual surveys were performed every summer between 25
166 June and 25 August (mostly in early August) to assess the presence or absence of calf at heel.
167 Because pre-weaning calf mortality typically occurs in the first days after birth, these behavioral
168 observations provide good measures of reproductive success [49].

169 On average, 42% of the females captured in April/May were observed in the following
170 summer but females experiencing high ROS_{utero} had a higher re-sighting probability than females
171 born under more favorable conditions (49% vs. 38%; $\chi^2_{(df=1)} = 14.99$, $p < 0.001$). Related to this,
172 53% of non-pregnant females were not observed during the following summer if they were born
173 after high ROS_{utero} compared with 66% for non-pregnant females born after low ROS_{utero} ($\chi^2_{(df=1)} = 6.69$, $p = 0.009$). In order to avoid bias in the analyses, we relied solely on summer
174 observations to estimate annual reproductive success.
175

176

177 **(d) Statistical analyses**

178

179 Statistical analyses were performed using R v. 3.1.2 R (<http://www.r-project.org>). All response
180 variables were individual-year observations. We used the ‘lme4’ library [50] for fitting
181 generalized linear-mixed models (GLMMs) with binomial errors and a logit link function. All
182 mixed models included female identity and year of sample collection as random effects to
183 control for the non-independence of repeated measure of the same female and unmeasured
184 sources of between-year variation. We used a backward selection procedure, testing successively
185 the first-order interactions and, if not statistically significant, the main effects of variables.
186 Statistical significance was assessed by likelihood ratio test and Wald statistics [51].

187 In most iteroparous species, fitness components initially increase with age and then
188 decrease after a certain age threshold (the onset of senescence). This onset of senescence is 7
189 years in both reproductive success and survival of female Svalbard reindeer (see Results). Thus,
190 to investigate late-life performance, our models only included the probabilities of reproductive
191 success and survival at 7 years and over. For reproductive success, we constructed a GLMM
192 containing ROS_{utero} and age (fitted as a linear or quadratic function) as the fixed effects of
193 interest. We included an interaction between ROS_{utero} and both age and its square to determine
194 whether reproductive senescence differed in relation to early-life environment. Age at last

195 observation was also included as fixed effect term to control for selective disappearance (the
196 non-random departure from the data set of individuals as age increase) so that age effect reflected
197 an unbiased estimate of within-individual change [52]. Age at last observation was retained in
198 the model independent of its statistical significance. To further characterize the breeding
199 environment, we included ROS in the previous winter (ROS_{current}) as this is strongly negatively
200 associated with reproductive success [42]. ROS_{current} was fitted as a continuous variable after a
201 log+1 transformation to reduce non-linearity [42]. We tested whether ROS_{utero} affected late-life
202 reproductive success through differences in costs of early reproduction by re-running our
203 previously selected model of reproductive success with the three-way interaction of the
204 proportion of years in which a female produced a calf between age at first reproduction and 6
205 years old, ROS_{utero} , and age. The full model of ‘late life’ survival included ROS_{utero} , age,
206 ROS_{current} and the interaction between ROS_{utero} and age. We analyzed survival by using capture-
207 mark-recapture (CMR) models [53] with E-surge [54] because of the imperfect detection of
208 individuals. Survival data included capture histories of 407 females. Following previous CMR
209 analyses in this population [47, 49], capture probability was allowed to vary between years.
210 Capture probability did not vary with ROS_{utero} ($\Delta\text{AIC} = 2.80$ compared with a time dependent
211 model). Due to small sample sizes at high ages we pooled data from females ≥ 14 years of age in
212 analyses of reproductive success, and data from females ≥ 12 years of age in analyses of
213 survival.

214 We tested whether there was any significant relationship between ROS_{utero} and
215 reproductive success during early adulthood by considering females aged between 2 and 6 years.
216 Our full GLMM included the effects of ROS_{utero} , age (fitted as a quadratic function), ROS_{current} ,
217 and age at last observation within this age class. Based on survival changes with age (see
218 results), we also tested the effect of ROS_{utero} on survival of yearling females (1 year olds) and
219 survival between 2 and 6 years after accounting for the influence of ROS_{current} .

220 We examined whether the relationship between pregnancy rate and body mass of young
221 females (between 2 and 6 years) varied according to environmental conditions experienced in
222 *utero* by assessing the evidence supporting an interaction between body mass adjusted to April
223 12 (the mean Julian date of the whole capture period) and ROS_{utero} in a GLMM. We also repeated
224 the analysis for each age between 2 and 6 separately using GLMs. To obtain a measure of effect
225 size, we compared predicted body mass at 50% probability of pregnancy between females that

226 experienced high vs. low ROS_{utero} .

227 In order to quantify the fitness consequences of ROS_{utero} , we built two Leslie matrix
228 models [55], one for each modality of ROS_{utero} . We entered the age-specific values of
229 reproductive success and survival, with their uncertainty, into the matrix models (electronic
230 supplementary material, figure S3) to obtain the asymptotic growth rate (λ , the mean fitness
231 sensu [56]) and its 95% confidence interval of each of these groups with bootstrap methods
232 (10000 simulations). Estimates of λ were approximately normally distributed and were compared
233 using the percentile method.

234

235 3. Results

236

237 (a) Age-specific variation in reproductive success and survival

238

239 Reproductive success increased with female age until about 5 years and then remained relatively
240 stable until 7 years before declining (figure 2a). A linear function of female age adequately
241 explained changes in reproductive success between 7 and 14 years (table 1). Survival between 1
242 and 2 years was around 0.80 (figure 2b). Survival slightly increased with age between 2 and 6
243 years (from about 0.90 to 0.95) and declined strongly after age 7 ($\chi^2_{(d.f. = 1)} = 32.64$, $p < 0.001$,
244 slope on a logit scale: -0.30 ± 0.05 , figure 2b).

245

246 (b) Senescence

247

248 Females aged ≥ 7 years born after high ROS_{utero} had 1.84 times lower chances of rearing a calf
249 than those born after low ROS_{utero} (table 1, figure 3). There was no evidence of an interaction
250 between age and ROS_{utero} on reproductive success of these females (table 1). Thus, females that
251 experienced poor conditions in early life did not suffer steeper rates of reproductive senescence.
252 We found no evidence for a significant interaction between average reproductive success
253 between 2 and 6 years and ROS_{utero} or age on late life reproductive success (early reproduction \times
254 ROS_{utero} : $\chi^2_{(d.f. = 1)} = 0.79$, $p = 0.37$; early reproduction \times age: $\chi^2_{(d.f. = 1)} = 1.70$, $p = 0.19$; early
255 reproduction \times $ROS_{utero} \times$ age: $\chi^2_{(d.f. = 1)} = 0.25$, $p = 0.62$). The correlation between early and late
256 reproductive success is positive rather than negative (slope = 0.66 ± 0.25 , $p = 0.007$). The effect

257 of ROS_{uter0} on reproductive success of older females was independent of the positive influence of
258 reproduction in early adulthood (electronic supplementary material, table S1). Annual survival
259 after age 6 was negatively influenced by $ROS_{current}$ ($\chi^2_{(d.f. = 1)} = 3.71$, $p = 0.05$, slope on a logit
260 scale: -0.36 ± 0.18). However, ROS_{uter0} did not have a significant effect fitted alone or in
261 interaction with age on survival ($ROS_{uter0} \times age$: $\chi^2_{(d.f. = 1)} = 0.44$, $p = 0.51$; ROS_{uter0} : $\chi^2_{(d.f. = 1)} =$
262 0.05 , $p = 0.81$).

263

264 (c) Performance during early adulthood

265

266 After accounting for a quadratic age effect and negative influence of $ROS_{current}$, we found no
267 effect of ROS_{uter0} on annual reproductive success of females aged between 2 and 6 years ($\chi^2_{(d.f. = 1)}$
268 $= 0.16$, $p = 0.68$; figure 4; electronic supplementary material, table S2). There was no
269 relationship between age at last observation and reproductive success of young females
270 (electronic supplementary material, table S2), regardless of ROS_{uter0} ($\chi^2_{(d.f. = 1)} = 0.01$, $p = 0.93$).
271 Neither $ROS_{current}$ nor ROS_{uter0} influenced the survival of young females (all $p > 0.20$). The
272 probability of survival between 1 and 2 years was estimated to be 0.79 (95% IC = (0.70, 0.86))
273 for females born after high ROS_{uter0} and 0.81 (95% IC = (0.75, 0.87)) for females born after low
274 ROS_{uter0} . Annual survival rate between 2 and 6 years was 0.94 for both groups.

275

276 (d) Pregnancy rate for a given body mass

277

278 The proportion of pregnant females between 2 and 6 years did not depend on ROS_{uter0} ($\chi^2_{(d.f. = 1)} =$
279 1.02 , $p = 0.31$, see also electronic supplementary material, figure S4). However, the relationship
280 between annual pregnancy rate and body mass varied according to ROS_{uter0} ($\chi^2_{(d.f. = 1)} = 7.41$, $p =$
281 0.006 , figure 5a). Most young females > 48 kg were pregnant. Below this mass, however,
282 females experiencing high ROS_{uter0} achieved higher pregnancy rate for a given body mass than
283 females born under more favorable conditions (figure 5a). To have a 50% chance of pregnancy,
284 young females born after low or high ROS_{uter0} weighted 43.7 ± 0.3 kg and 41.2 ± 0.6 kg
285 respectively. This corresponded to an average difference of 2.5 kg. When we repeated the
286 analysis for each age between 2 and 6, we found that females born after high ROS_{uter0}
287 consistently had a lower mass at 50% pregnancy probability than females born after low ROS_{uter0}

288 except at 2 years of age when only 11% of the females were pregnant (figure 5b, electronic
289 supplementary material, figure S4).

290

291 (e) Fitness consequences of ROS_{utero}

292

293 Leslie matrix models indicate that the asymptotic growth rate (λ) of cohorts born under poor
294 conditions was only marginally lower than that of cohorts born under favorable conditions, with a
295 near complete overlap in confidence limits (high ROS_{utero}: $\lambda = 1.04$, 95% IC = (0.96, 1.09); low
296 ROS_{utero}: $\lambda = 1.07$, 95% IC = (1.03, 1.10)).

297

298 4. Discussion

299

300 We found that early-life environmental conditions influence reproductive success of female
301 Svalbard reindeer but in a highly age-dependent manner. The negative effects of rain on snow *in*
302 *utero* (ROS_{utero}) on annual reproductive success occurred only among females aged 7 years and
303 older. Females experiencing high ROS_{utero} were able to maintain the same annual reproductive
304 success between 2 and 6 years as phenotypically superior conspecifics born after low ROS_{utero}.

305 Young females born after high ROS_{utero} engaged in reproductive events at a lower body mass
306 than those born after low ROS_{utero}, which is consistent with the internal predictive adaptive
307 response (internal PAR) hypothesis. Furthermore, mean fitness of females that experienced poor
308 environmental conditions in early life was comparable to that of females exposed to more
309 favorable conditions.

310 Many studies have shown that individuals born in poor environmental conditions are at
311 permanent reproductive disadvantage regardless of their adult environment [21, 22, 25, 58], the
312 so-called reverse silver spoon effect [12, 13]. However, such effects are not universal in food-
313 limited environments. For instance, captive female guppies compensated for experimental food
314 restrictions during the juvenile stage by accelerating growth rates in the adult stage and achieved
315 the same reproductive success than those that experienced high food levels as juveniles [17].
316 Here, we show that young female Svalbard reindeer mitigated the negative long-lasting effects of
317 ROS_{utero} through a change in reproductive tactic. Thus, females that experienced poor conditions
318 *in utero* were able to maintain the same reproductive success through their first 6 years of life as

319 phenotypically superior females who experienced good conditions *in utero*. The negative impact
320 of ROS_{utero} on reproductive success appeared only from 7 years of age. This is an important point
321 with respect to fitness consequences of early-life conditions because in a growing population, as
322 is the case here [45], offspring produced early in life contribute more to fitness than do offspring
323 produced late in life [59]. Hence, by using Leslie matrix models, we found that asymptotic
324 growth rate, a measure of mean fitness, was comparable between individuals exposed to
325 contrasting ROS_{utero} . A different conclusion would probably have been reached with a measure of
326 lifetime reproductive success, which neglects timing of reproduction within the life cycle. As a
327 cautionary note, however, we entered the same estimate of calf winter survival for both groups in
328 matrix models, whereas we do not know whether this parameter varied with ROS_{utero} .
329 Unfortunately, information on calf winter survival is not available because calves are marked for
330 the first time at ca 10 months of age.

331 How might the delayed effects of ROS_{utero} on reproductive success that we report arise?
332 First, this seems to correspond to a direct effect of ROS_{utero} rather than differential costs of early
333 reproduction between individuals born under contrasting ecological conditions. Indeed, we report
334 a lack of interaction between early-life reproduction and ROS_{utero} on late-life reproductive
335 success. Instead, high early-life reproductive output was positively associated with subsequent
336 age-specific reproductive success. In red deer, the effects of early life reproduction and
337 population density in year of birth on reproductive senescence rates were also independent of one
338 another [24]. However, contrary to Svalbard reindeer, female red deer that produced more
339 offspring during early adulthood showed higher rates of reproductive senescence [24, 60] as
340 predicted by the disposable soma theory [32, see 33 for a review]. Tests for trade-offs between
341 allocation to early reproduction and late-life performance can yield positive rather than negative
342 correlations (e.g. [61, 62]), because some individuals consistently acquire a large amount of
343 resources such that they are able to allocate much energy to several functions without suffering
344 from any costs across their lifespan [63]. An explanation for direct effects of ROS_{utero} on late-life
345 reproductive success is that under nutrition during gestation affects gene expression associated
346 with changes in the physiology and metabolism of the offspring. The effects of epigenetic
347 modifications *in utero* on performance may not manifest until later in life [64]. We cannot,
348 however, exclude the possibility that the physiological changes occur during post-natal
349 development as females in poor condition can allocate less energy to offspring through lactation

350 after experiencing high ROS the preceding winter. Irrespective of the precise mechanism, our
351 study provides evidence of intergenerational climate impacts on reproduction in a wild
352 population.

353 There are a few studies conducted in the laboratory which support the internal PAR
354 hypothesis [15]. For instance in the rat, maternal caloric restriction during pregnancy led to early
355 pubertal onset of offspring [65]. We cannot measure the influence of ROS_{utero} on age at first
356 reproduction of female reindeer because this life-history trait is unknown for most of them.
357 Rather, we investigated how the mass-specific probability of pregnancy for young females varies
358 with environmental conditions in early life. Thus, we take into account biological constraints
359 imposed by body mass on pregnancy rate. The relationship between maturity and size is often
360 considered for studying the potential evolutionary consequences of fishing. For example, before
361 Canadian populations of Atlantic cod (*Gadus morhua*) collapsed in the 1990s, young females
362 showed a decline over time in size at which the probability of maturing was 50%, supporting the
363 idea that fishing may select for and cause evolution of maturity at smaller size [66]. In red deer,
364 females conceived at higher body mass in high density populations than in low density
365 populations likely to reduce the risk of mortality due to early reproduction when resources are
366 scarce [67]. Our results show that substantial differences can exist among individuals in a
367 population. Young females (2-6 years old) born after high ROS_{utero} achieve a 50% probability of
368 pregnancy at about 2.5 kg lower body mass than females born after low ROS_{utero} . Young females
369 that experienced poor conditions in early life engage in reproduction at lower body mass possibly
370 in anticipation of their reduced reproductive performance in later life.

371 Climate change is particularly pronounced in the high Arctic and ROS events are
372 predicted to become increasingly frequent [36, 68]. These extreme weather events have major
373 ecosystem wide implications as they synchronize population fluctuations across the entire
374 community of terrestrial species on Svalbard, including Svalbard reindeer [69]. ROS events have
375 immediate negative effects on body mass and reproductive success of adult female reindeer [42,
376 45], as well as on survival of older females (this study). However, asymptotic growth rate of
377 cohorts born after high ROS_{utero} was comparable to that of cohorts born after low ROS_{utero} ,
378 suggesting that the long-term delayed effects of ROS_{utero} on reproductive success had no major
379 demographic consequences. The reproductive tactics of females born under poor environmental
380 conditions have the potential to limit some of the negative effects of climate change. To date,

381 most studies of climate change impacts have focused on plasticity in adulthood such as the date
382 of egg laying [70] or hibernation emergence [71]. Our findings highlight the need to consider the
383 role of developmental plasticity in the ability of wild populations to track, buffer and adapt to
384 environmental changes.

385

386 **Ethics.** All capture and live animal handling procedures were performed under licences from the
387 Norwegian Food Inspection Authority and its predecessor the Norwegian National Research
388 Authority.

389 **Data accessibility.** Data available from the Dryad Digital Repository:

390 <http://dx.doi.org/10.5061/dryad.fp505>

391 **Competing interests.** We declare we have no competing interests.

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402

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404

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- 576

577 **Table**

578

579 Table 1. Generalized linear mixed model of the probability of reproductive success based on 417
 580 observations of 157 female Svalbard reindeer aged 7 years and over. Parameter values are given
 581 for the final model, excluding non-significant terms except age at last observation. Interactions
 582 are denoted by \times . We reported standardized regression coefficients for the final model by first
 583 centering and then dividing all continuous variables by 2 s.d [57].

Analysis of deviance	χ^2	d.f.	p-value
$ROS_{utero} \times age^2$	1.14	1	0.29
age^2	0.13	1	0.72
$ROS_{utero} \times age$	0.30	1	0.58
ROS_{utero}	5.05	1	0.02
$\log(ROS_{current} + 1)$	4.50	1	0.03
Age	3.95	1	0.04
final model	Estimate	s.e.	p-value
intercept \dagger	-0.312	0.330	0.34
age at last observation	-0.183	0.305	0.54
$\log(ROS_{current} + 1)$	-1.255	0.533	0.02
Age	-0.608	0.308	0.04
ROS_{utero}	0.612	0.275	0.02

584 \dagger Females born under high ROS_{utero} were considered as reference.

585

586 **Figures captions**

587

588 Figure 1. High ROS_{uter0} has a long-lasting negative influence on body development of female
589 Svalbard reindeer. Differences (\pm s.e.) in body mass (BM in kg) and skeletal size (SS in mm)
590 between calves (1 year, $n = 445$) and adults (4-9 years, $n = 849$) that experienced low ROS_{uter0}
591 and those that experienced high ROS_{uter0} . All differences are statically significant ($p < 0.001$). We
592 used linear models to estimate values for calves with ROS in the current year as covariate in the
593 body mass model. We used linear mixed models to estimate values for adults with year and
594 female identity as random factors. We also included $ROS_{current}$ and Julian date of capture as
595 covariates in the model of adult body mass.

596

597 Figure 2. Age-specific probability (\pm s.e.) of reproductive success and survival in female
598 Svalbard reindeer. a) Lines are predicted age curves from a generalized additive mixed model for
599 females with different ages at last observation, as indicated by the age where the lines end.
600 Sample size for each age is indicated at top of the figure. b) The line represents the predicted
601 values obtained from a generalized linear model with a cubic effect of age.

602

603 Figure 3. Relationship between reproductive success and age for female reindeer aged 7 years
604 and over that experienced high (triangles and solid line) or low (filled circles and dashed line)
605 ROS_{uter0} . The lines represent model predictions for females with different ages at last
606 observation, as indicated by the age where the lines end. Age specific estimates \pm s.e. (points
607 with errors bars) are obtained by fitting age as a factor. The number of individuals of each group
608 for each age is indicated at top of the figure.

609

610 Figure 4. Relationship between reproductive success and age for female reindeer aged 2-6 years
611 that experienced high (triangles) or low (filled circles) ROS_{uter0} . The number of individuals of
612 each group for each age is indicated at top of the figure.

613

614 Figure 5. a) Pregnancy rate as a function of body mass and the quality of early environment (high
615 ROS_{uter0} : triangles and solid line, low ROS_{uter0} : circles and dashed line) in young female (2-6
616 years of age) Svalbard reindeer. Lines show the predicted values and points indicate the raw data

617 (n = 1050). b) Age-specific mass \pm s.e. at 50% pregnancy probability for female reindeer that
618 experienced high (open triangles) or low (filled circles) ROS_{utero} .

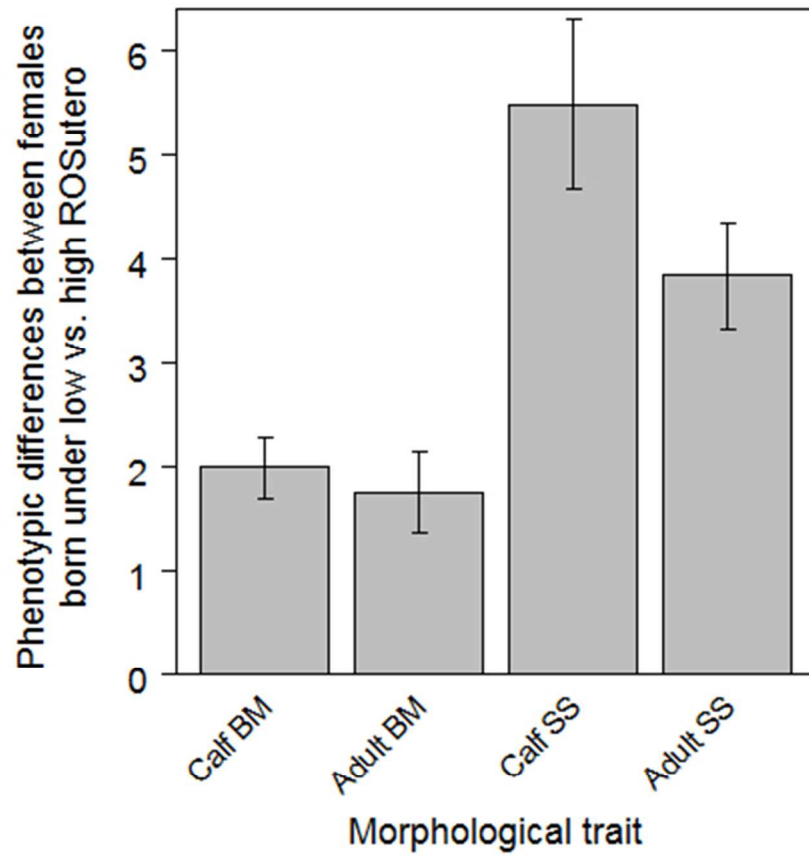


Figure 1

169x169mm (72 x 72 DPI)

a)

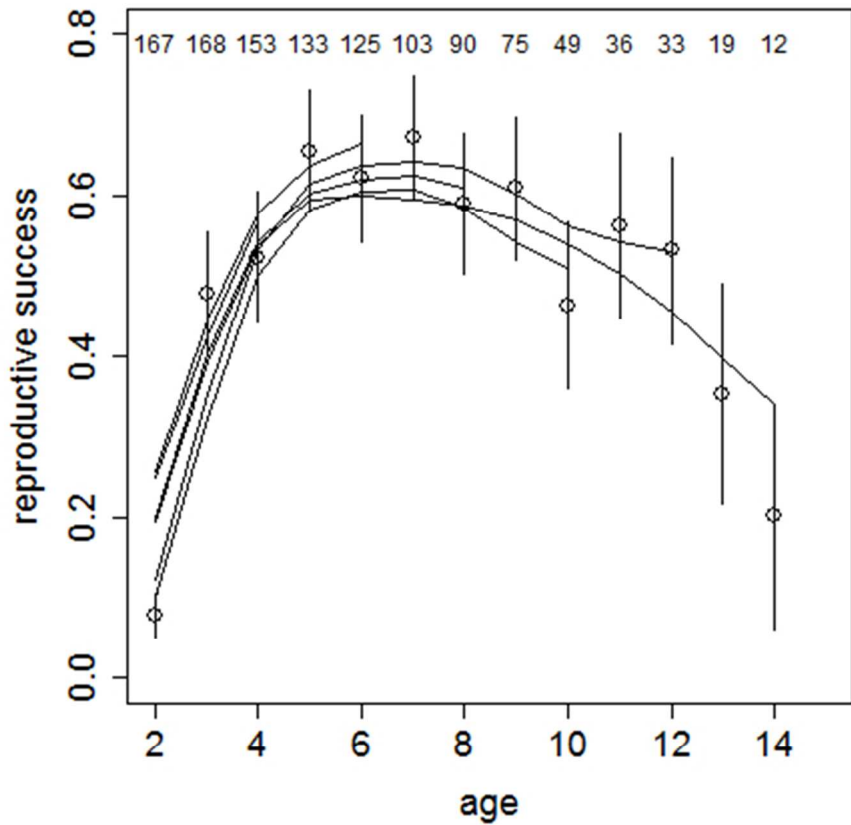


Figure 2a

169x169mm (72 x 72 DPI)

b)

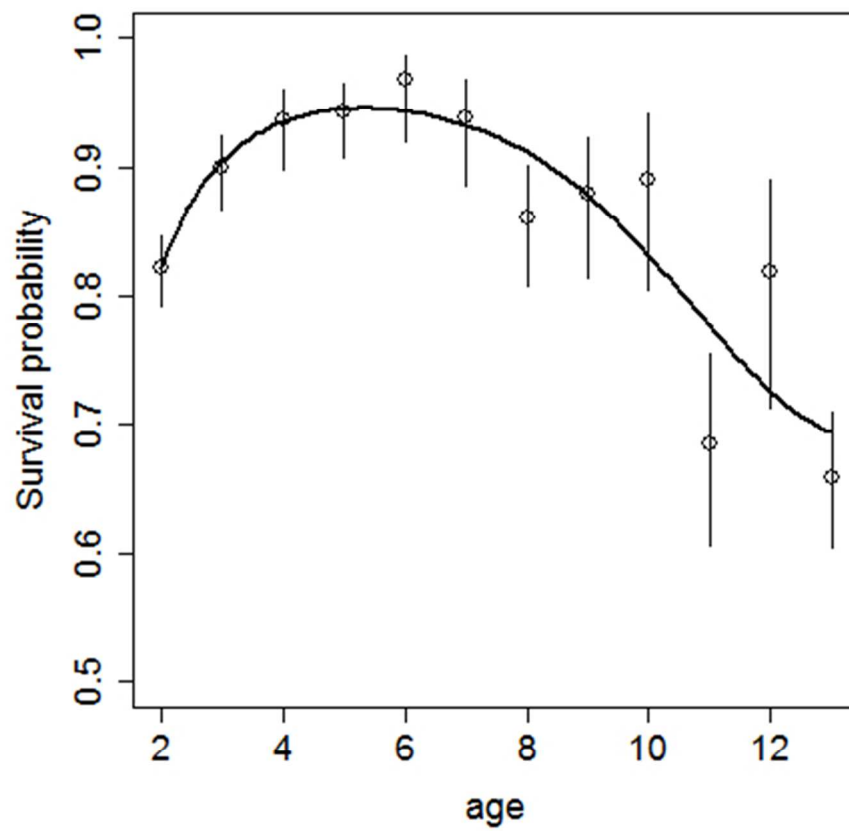


Figure 2b

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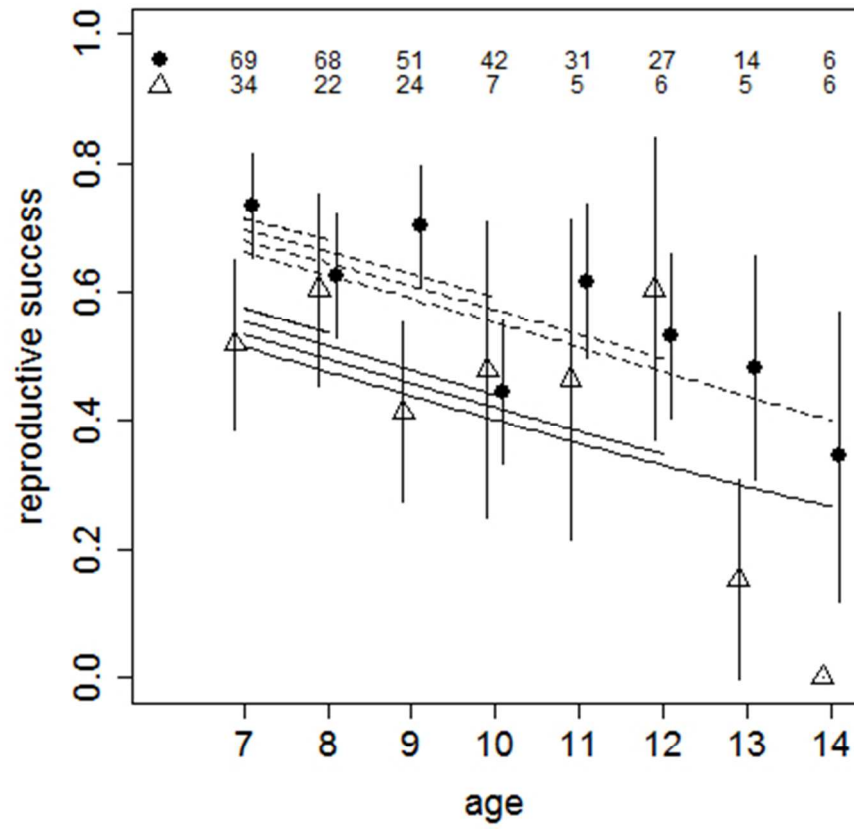


Figure 3

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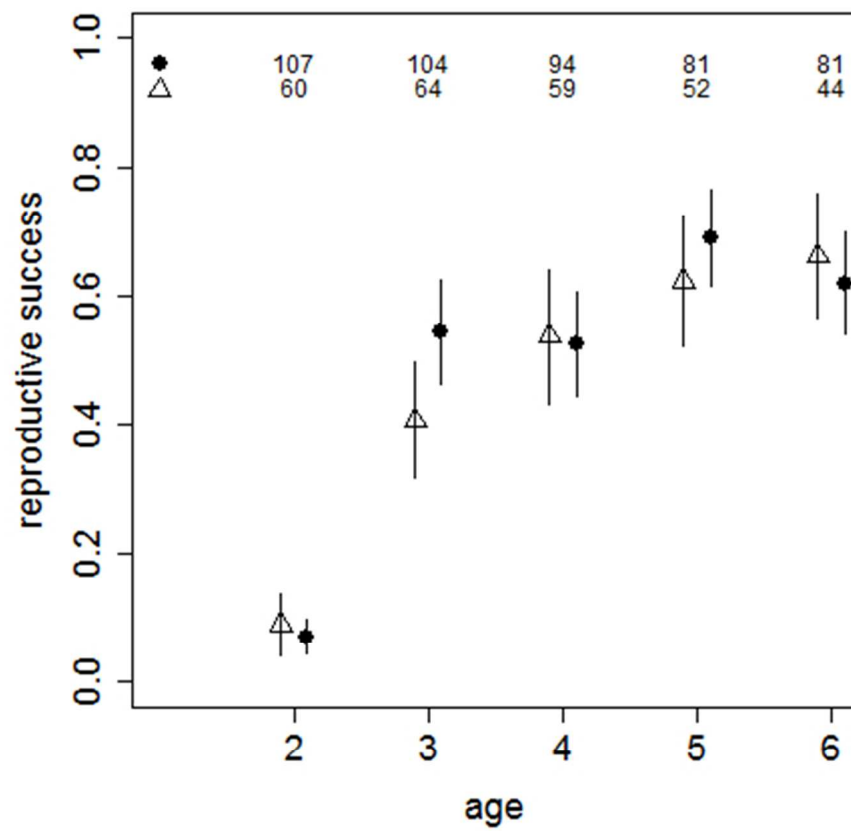


Figure 4

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a)

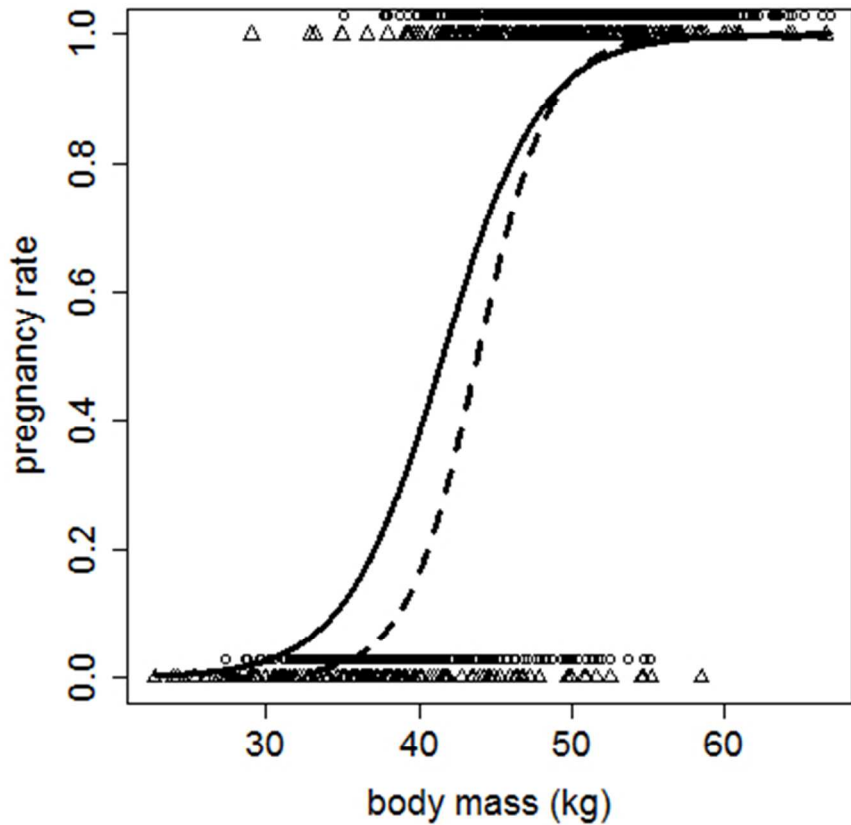


Figure 5a

169x169mm (72 x 72 DPI)

b)

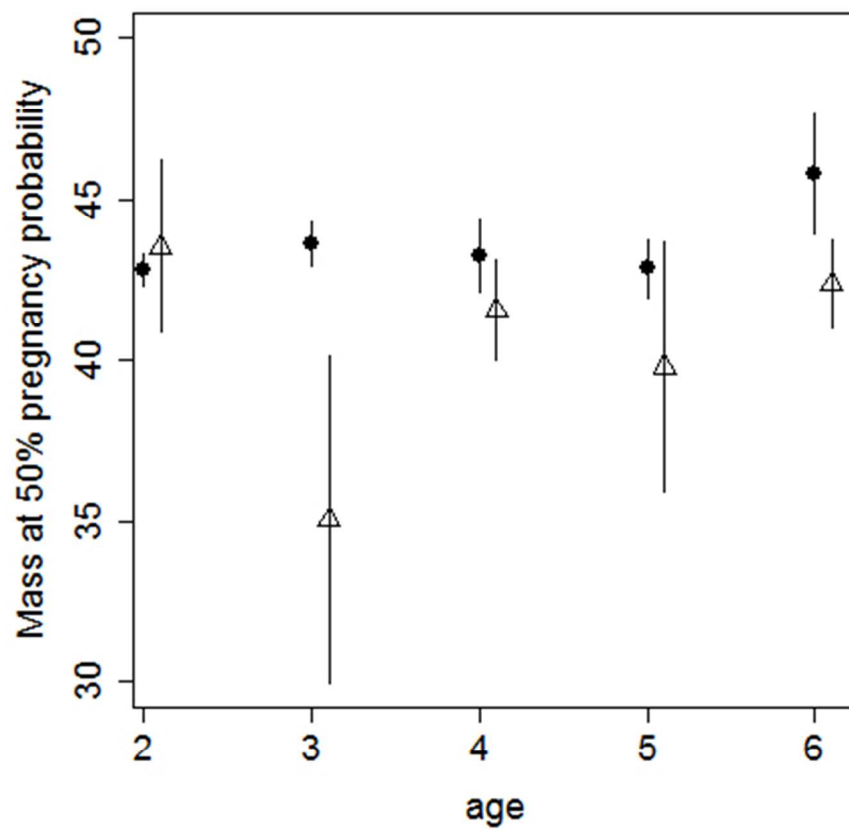


Figure 5b

169x169mm (72 x 72 DPI)