Early-life conditions determine the between-individual heterogeneity in plasticity of calving date in reindeer

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Abstract

16   Abstract

17   1. Phenotypic plasticity has become a key-concept to enhance our ability to understand the

18   adaptive potential of species to track the pace of climate change by allowing a relatively

19   rapid adjustment of life history traits.

20   2. Recently, population-level trends of an earlier timing of reproduction to climate change have

21   been highlighted in many taxa but only few studies have explicitly taken into consideration

22   between-individual heterogeneity in phenotypic plasticity.

23   3. Using a long-term data of a semi-domesticated reindeer (*Rangifer tarandus*) population, we

24   demonstrated that females differed greatly in their mean calving date but only slightly in the

25   magnitude of their plastic response to the amount of precipitation in April. We also showed

26   that despite the absence of a population trend, females individually responded to the amount

27   of precipitation in April by delaying their calving dates.

28   4. Females' calving date under average climatic conditions was best predicted by their

29   birthdate, their physical condition in March-April-May before their first calving season and

30   by their first calving date. The degree of their phenotypic plasticity was not dependent on

31   any of the females' attributes early in life tested in this study. However, females who delayed

32   their calving dates in response to a higher amount of precipitation in April slightly produced

33   less calves over their reproductive life.

34   5. These findings confirmed that early life conditions of female reindeer can shape their

35   phenotypic value during reproductive life, supporting the importance of maternal effects in

36   shaping individuals' lifetime reproductive success. Whether females differed in the

37   magnitude of their plastic response to climatic changes has received contrasted responses for

38   various ungulate species. This calls for more research to enhance our understanding of the

39   underlying mechanisms leading to the complexity of plastic responses among populations to

40   cope with current climate change.

Introduction

Phenotypic plasticity, defined as the expression of several phenotypes by a single genotype when facing heterogeneous climatic conditions, has become a key-concept in understanding how animal species will be able to track large-scale environmental processes, such as climate change (Boutin & Lane, 2014). Phenotypic plasticity allows species a relatively rapid adjustment of morphological and life history traits to climatic changes (Boutin & Lane, 2014). Under the current context of climate change, the timing of reproduction is one key life history trait that species would need to adjust to ensure their viability. Indeed, an advantageous timing of reproduction will generally ensure that young are born at the time of the year best suited for their survival (Festa-Bianchet, 1988; Gaillard, Delorme, Tullien, & Tatin, 1993), which determine the population's recruitment rate (Berger, 1992; Post & Klein, 1999) and thereafter the population dynamics. Recently, such timing of reproduction was broadly shown to vary at the population level with climatic changes observed the last decades between different groups of species (bird: Visser, van Noordwijk, Tinbergen, & Lessells, 1998; Bourret, Bélisle, Pelletier, & Garant, 2015; amphibian: Blaustein et al. 2001; fish: Asch 2015; mammal: Réale, McAdam, Boutin, & Berteaux, 2003; Post and Forchhammer 2008; Moyes et al. 2011; marine species: review in Poloczanska et al. 2013). However, on top of those population-level trends, knowing how changing timing of reproduction vary between individuals in response to climate change has not received enough attention, yet very much needed for a better understanding of the evolutionary consequences of the changes.

At the population level, observed correlations between climate and phenotype are thought to be induced by phenotypic plasticity at the individual-level. For example, Przybylo, Sheldon, & Merila (2000) reported laying date between and within females collared flycatchers (*Ficedula*

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albicollis) to vary in response to the NAO index, while Réale et al. (2003) found that the advance in parturition date to increased food availability of female red squirrels (*Tamiasciurus hudsonicus*) was a result of phenotypic changes within generations. According to these studies, such a population-level change in breeding time to the environment could be explained to a large extent by maternal plasticity as the responses across and within individuals were similar. However, the degree to which females varied in their plastic response was not explicitly quantified. To date, only few studies have explicitly examined between-individual heterogeneity in phenotypic plasticity, and most found that females differed in the way they adjusted breeding time in response to climate change (bird: Brommer, Merilä, Sheldon, & Gustafsson, 2005; Nussey, Postma, Gienapp, & Visser, 2005; ungulate: Nussey, Clutton-Brock, Elston, Albon, & Kruuk, 2005). To clarify this issue, Nussey et al. (2005) applied the linear reaction norm approach (Brommer et al., 2005; Nussey, Postma, et al., 2005) on a red deer (*Cervus elaphus*) population, stating that an individual's phenotypic response to climatic changes can be estimated using regression coefficients of models describing the variation in the value of a certain phenotypic trait along a climatic gradient. We can then differentiate an individual's intercept (reflecting the expected trait value in the average climate) and slope (the plastic response to the climatic gradient). Two main population-level phenotypic plastic responses to climatic variability have been described by Pigliucci (2001; see Figure 1.2d, e in Pigliucci 2001). In the first one, all individuals of a population respond in the same way and vary in their intercept but not in their slope (scenario 1; Fig. S1a adapted from Figure 1.2d in Pigliucci 2001). In the second one, all individuals will show different plastic responses to climate change and will therefore vary in their slope (scenario 2; Fig. S1b adapted from Figure 1.2e in Pigliucci 2001). Where individual intercepts show no variation but slopes do vary or where intercepts and slopes both vary and also covary, levels of phenotypic variance in the trait measured is predicted to change across the climatic gradient (Postma & van Noordwijk, 2005).

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91 The presence of an individual by environment interaction (I×E) might also determine the

92 adaptive potential for change in the average plastic response of the population (Nussey, Wilson,

93 & Brommer, 2007). Distinguishing which of those patterns is occurring in an animal population

94 is therefore determinant for our understanding to any population's ability to cope with climate

95 change and has important implications for population dynamics (Nussey, Clutton-Brock, et al.,

96 2005; Przybylo et al., 2000; Réale et al., 2003).

97   In a theoretical framework, an individual is expected to follow its optimal trait-climate

98 trajectory by responding to the climate depending on its physical condition (Roff, 1992).

99 However, understanding how the between-individual differences in phenotypic plasticity are

100 explained by climatic conditions or physiological state is largely unknown. If a large

101 intraspecific difference in body mass exists, then the second pattern of phenotypic plasticity

102 (scenario 2; Fig. S1b) is usually expected in those species (Skogland, 1983). The social

103 hierarchy in reindeer causes large differences in resource access (e.g. food), with high-ranked

104 females having access to the best food patches (Skogland, 1983). As a consequence, reindeer

105 present large intraspecific differences in size and body mass (Skogland, 1983, 1984). In

106 addition, maternal characteristics were shown to exert a great influence on calving date (Adams

107 & Dale, 1998; Cameron, Smith, Fancy, Gerhart, & White, 1993; Flydal & Reimers, 2002;

108 Mysterud, Røed, Holand, Yoccoz, & Nieminen, 2009; Rowell & Shipka, 2009). As such, a

109 plastic response of birthdate to climatic variability is expected following a pattern where

110 females will differ both in their intercept and in their slope values (scenario 2; Fig. S1b).

111   To further dissect the average plastic response of the population from the individual's

112 reaction norms to climatic changes, the within-subject centering method for climatic variables

113 can be employed (van de Pol & Wright, 2009). This technique was developed to separate

114 individual heterogeneity from population trend, while considering that each female might

115 experience a different set of climatic conditions. The between-individual effect for a certain

climatic variable would indicate a population-level, evolutionarily fixed plasticity of calving

date to this climatic variable (i.e. certain phenotypes are consistently found more frequently in

certain climatic conditions). If, in addition, a within-individual effect of the same climatic

variable was found, it would indicate that females alter their calving date in response to that

variable within their reproductive lifetimes. Van de Pol and Wright (2009) also proposed a

method to test if the direction of the individual- and population-level trends was the same or

not. Accordingly, four different scenarios have been described (Fig. 1 and Table S1), that are

important in understanding how species will be able to cope with their changing climate. The

within- and between-individual effects of a particular trait in response to a climatic gradient

highlight its flexibility in a population, and therefore represents alternative adaptive outcomes

of selection (van de Pol & Wright, 2009). In three of the four scenarios (Fig. 1a, b, d), a

population-level response to the climatic gradient is observed but do not necessarily mean that

individuals are responding plastically to climate change (Fig. 1b). In such case, plasticity in

calving date is observed at the population-level but the absence of phenotypic plasticity at the

individual level would cause females to be maladapted in the future regarding the ongoing

climate change. Conversely, individuals might be responding to climate change, while a

population-level trend might be null due to a low plasticity in the phenotypic trait along a

climatic gradient (Fig. 1c). Population-level analyses therefore appear insufficient in inferring

the ability of individuals to alter the expression of a phenotypic trait in response to climatic

conditions and thus the potential for individuals to track their changing climate. Furthermore,

an individual-level response might also mask the fact that slopes between females can differ

(e.g. female 1 might have a negative slope, while female 3 might have a positive slope, see Fig.

1a, c, d). The population- and individual-level trends therefore demand to be studied while

accounting for a potential between-individual heterogeneity in plasticity. In our study, we

predict that if females are all in a good enough physiological state to respond to climatic

variability (Nussey, Clutton-Brock, et al., 2005), an individual-level response to climate change would be observed (Fig. 1a, c, d), in addition to an individual heterogeneity in plasticity as stated above.

Using records from a long-term intensive study of a semi-domesticated reindeer population situated in Kaamanen, northern Finland, the aims of this study were the following. (1) To investigate if there is a between-individual heterogeneity in plasticity of calving dates in response to climatic variability and to assess which pattern of phenotypic plasticity among the two scenarios adapted from Pigliucci (2001) is occurring in this reindeer population. (2) To assess whether the within- and between-individual responses of calving date to climatic variables go in the same direction (van de Pol & Wright, 2009). (3) To determine the females' attributes shaping or explaining the pattern of phenotypic plasticity observed; and (4) to determine if the among-individual heterogeneity in phenotypic plasticity can lead to fitness consequences. Climatic conditions while *in utero* and early in life usually shape the total lifetime reproductive success (Forchhammer, Clutton-Brock, Lindström, & Albon, 2001; Kruuk, Clutton-Brock, Rose, & E., 1999; Post & Stenseth, 1999). Therefore, we separately assessed if mothers' physical condition during pregnancy and/or females' own physical condition at birth and/or at age of first calving would shape the between-individual heterogeneity in phenotypic plasticity, and if further consequences on the reproductive success of females were observed.

Material and methods

Study area and reindeer population

The herd studied consists of about 100 animals every year (including males, females and calves) from a semi-domesticated reindeer population at the Kutuharju field reindeer research station in Kaamanen, northern Finland (69°N, 27°E). The herd is free ranging most of the year

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165 in two large fenced enclosures, the north-west section (Lauluvaara ~ 13.8 km²) and the south-

166 east section (Sinioaivi ~ 15 km²). After the mating season in late October the animals are

167 gathered and taken to a winter grazing area (15 km²) where they can graze freely on natural

168 pastures. Supplemental feed (pellets and hay) was given to the animals in late winter, in addition

169 to natural pastures. After harsh winters, the amount of supplemental feed was higher than this

170 average level of feeding. We therefore excluded the calving dates from females that have been

171 subject to experimental manipulations requiring extra-feeding, as this may affect between-

172 individual heterogeneity in phenotypic plasticity of calving date to climatic conditions. By the

173 end of winter, females are transferred into a calving enclosure (approximately 0.5 km²) where

174 newborn calves are captured, weighed, sexed and marked with ear tags. The enclosure is

175 surveyed daily during the calving season that occurs mainly from mid-May to end of May

176 (Eloranta & Nieminen, 1986), so that calving date is known for all individuals and has been

177 recorded since 1970.

178 *Climatic variables*

179 The daily recorded values of temperature, precipitation and snow depth from 1970 to

180 2016 were obtained from three weather stations (Utsjoki, Ivalo airport and Nellim) in northern

181 Finland (68°N, 27°E) from the Finnish Meteorological Institute. The weighted mean by the

182 distance from the weather station to our study site was then used to estimate the daily values of

183 local climate at our study site with as much reliability as possible. The temperature was used as

184 a monthly average, while the amount of precipitation was summed over a month. Precipitation

185 can be either rainfall or snowfall depending on the temperature. From the daily snow depths, a

186 snow depth index (SDI) was calculated as the cumulative sum of daily snow depths on the 15th

187 day in each month.

Females' attributes in early life

189   Eleven female's attributes were used in the analyses, six of which were estimated at birth

190   and five at first calving. (1) The attributes of a female at birth included: the birth weight, year

191   of birth, birth date, and the mother's physical condition estimated in fall, winter and early

192   spring. (2) The attributes at first calving included: the female's age, physical condition in fall,

193   winter and early spring, and the calving date of her first calf. Thanks to the long-term records

194   of the herd demography and the use of ear tags on females (affixed at birth) allowing unique

195   identification and coloured collars fitted on their mother, we could track down their conditions

196   at birth and at first calving. Factors linked to maternal physical condition in reindeer interact

197   with each other so that older individuals tend to be heavier (Mysterud et al., 2009). Therefore,

198   we used a female body condition index (BCI) to consider effects of both female body weight

199   and female age on calving date at once in the models while avoiding multicollinearity between

200   these two highly correlated variables, as an age-specific residual body mass (see Weladji,

201   Holand, Steinheim, & Lenvik, 2003). To also account for the reported senescence in female

202   reindeer from this population (Weladji et al., 2010), we extracted the residuals from the

203   quadratic forms of the relationship between females' body weight and females' age. The

204   females' physical condition variable included in the base models (described below) to test H1

205   and H2 was calculated as the average of the 12 body condition indexes of a specific female over

206   the year preceding the calving season (year *t* from January to May and year *t* − 1 from June to

207   December). For the analyses testing H3, the mothers' and females' BCI was averaged for three

208   periods: fall before the rut period the previous year (September-October), winter (December-

209   January-February) and early spring before the calving season (March-April-May). This allowed

210   to specifically test which period's BCI of the mother or of the female (preceding her first calving

211   season) had the greatest influence in shaping among-individual heterogeneity in plastic

212   responses.

213   *Fitness attributes*

214   To estimate the females' reproductive success as an index of her fitness, we used three

215   different attributes, such as the body weight of her calves, the first-summer survival of her

216   calves and the cumulative number of calves that the female produced over her reproductive life.

217   The causes of death of a calf excluded from the analyses were those with 'no information' or

218   'slaughtered'. The values for the survival of a calf ranged from 0: dead during calving season

219   to 1: survived to autumn.

220   *Statistical analyses*

221   From the original dataset of reindeer calving dates of the Kutuharju herd used by Paoli,

222   Weladji, Holand, & Kumpula (2018), only data from females with available records for at least

223   four calving events (1,770 calving dates from 272 females, on average 6.51 ± 1.90 calving dates

224   per female) were kept in the analyses. Four calving events allowed to obtain an individual slope

225   estimate reliable enough to reflect a possible individual plastic response to its changing climate.

226   Moreover, the analysis restricting the data to females with 2 calving records or more (≥ 2

227   calving dates), 3 or more (≥ 3 calving dates), 4 or more (≥ 4 calving dates) yielded similar

228   results (See Table S2). Among the 272 females, 17.3% had 4 calving records, 17.6% had 5

229   calving records, 18.8% had 6 calving records, 17.3% had 7 calving records, 21.3% had between

230   8 to 9 calving events and 7.7% had 10 or more calving dates. All calendar dates were converted

231   into Julian days since 1 January for analysis (data available from 1970 to 2016). All continuous

232   explanatory variables were standardized (mean = 0, SD = 1) prior to inclusion in the models

233   (Pinheiro & Bates, 2000). We also examined whether or not there were consistent among-

234   individual differences in calving date by computing the repeatability in calving date (also

235   known as the intraclass correlation coefficient, ICC, Wolak, Fairbairn, & Paulsen, 2012). The

236   repeatability was calculated by dividing the variance in calving date due to differences among

237   individuals by the total phenotypic variance using the R package 'ICC' (Wolak et al., 2012).

238   Analyses were performed in R 3.4.1 (R Development Core Team, 2017).

239   Individual differences in mean calving date (intercept) and between-individual heterogeneity in

240   phenotypic plasticity (slope) (H1)

241   Given the previous results from Paoli et al. (2018), we constructed three base models to

242   explain variation in calving date. Here, (1) individual identity (ID) and year of study were

243   included as multi-level random effects to control for repeated measures and to account for

244   between-year variations (Kruuk et al., 1999) and; (2) the proportion of males present in the herd

245   the preceding mating season (PM) and the yearly body condition index of females (BCI) were

246   included as fixed-effect factors to control for their respective effects on calving date (Cameron

247   et al., 1993; Cook et al., 2004; Flydal & Reimers, 2002; Holand et al., 2002; Mysterud et al.,

248   2009). Then, the same climatic variables reported to be important in explaining calving date in

249   (Paoli et al., 2018) were included in three separate models: mean temperature in May (*T°May*)

250   and precipitation in April (*PrecApril*) for model 1, mean temperature in April-May (*T°April-

251   May*) and *PrecApril* for model 2 and *T°May* and snow depth index (SDI) in April (*SDIApril*)

252   for model 3. As an addition to Paoli et al. (2018) and Nussey, Clutton-Brock, et al. (2005), we

253   applied a within-subject centring method by subdividing the climatic variables into a within-

254   individual (β_W) and a between-individual (β_B) component (see the detailed method in the next

255   paragraph) to consider that not all females have experienced the same set of climatic variables.

256   We further tested our models for multicollinearity by calculating the variance inflation factor

257   (VIF) of the predictor variables used in each model. Multicollinearity was not an issue since all

258   VIF were < 3 (Zuur, Leno, & Elphick, 2010).

259   To test our first hypothesis, we then investigated the presence of between-individual

260   heterogeneity in plasticity (i.e. differences in slopes across individuals), as an individual by

261   environment interaction (IxE) with a random regression analysis (Nussey et al., 2007). For each

262   of the base models, the fixed effects were kept unchanged in the model while the mixed model

263   structure described above was modified to test patterns of heterogeneity in individual plasticity

264   of calving date (scenario 1 versus scenario 2, Fig. S1). More precisely, a random effect on

265   females' slopes of calving date to the β_W component of climatic variables considered can be

266   fitted in a mixed model (Bourret et al., 2015; Nussey, Clutton-Brock, et al., 2005). In this case,

267   ID estimates the variance component due to between-individual differences in their mean

268   calving date in the average climate (intercept), while the random interaction term estimates the

269   variance component resulting from differences between females in their calving date - climate

270   relationship (slopes). A statistically significant difference in deviance between LMMs with and

271   without a random slope term for β_W component of climatic variables would indicate that females

272   differ in their plastic response of calving date to climatic variables, allowing discrimination

273   between scenario 1 (Fig. S1a) and scenario 2 (Fig. S1b). Such difference in deviances and

274   increase in structure complexity of random effects was statistically tested by performing

275   likelihood ratio tests (LRT, Pinheiro & Bates 2000), including random slopes with climatic

276   variables (IxE). The analyses performed used Linear Mixed-effects Models (LMMs), by

277   running the lmer-function in the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015,

278   <www.r-project.org>).

279   Within- and between-individual response of calving date to climatic variability (H2)

280   To test our second hypothesis, we applied the within-subject centering method on our

281   climatic variables, obtained by the following equation (van de Pol & Wright, 2009):

282   $y_{ij} = \beta_0 + \beta_W(x_{ij} - \bar{x}_j) + \beta_B \bar{x}_j + u_{0j} + e_{oij}$ (1)

283   where β_0 represents the constant intercept of the equation; u_{0j} the random individual intercept

284   and e_{oij} the residual error term. The between-individual effect β_B for each female was

285   calculated as the mean of all observation values of a specific climatic variable she has

286   experienced over her lifetime $\bar{x}_j$ (reflecting the population trend). The within-individual

287   component β_W was calculated by subtracting the female's mean value $\bar{x}_j$ from each observation

288   value x_{ij} for that climatic variable (reflecting individual plasticity). The slope for the effect of

289   a specific climatic variable on calving date at the population-level was therefore given by β_B,

290   while it was given by β_W at the individual-level. We ran the base models by including as fixed

291   effects the within-individual (β_W) and between-individual (β_B) components of the climatic

292   variables present in each model (see Table 1). As random effects, the random intercept on Year

293   was included, along with the random intercept and/or the random slope on ID. If a between-

294   individual heterogeneity in the slope was previously found when testing H1, the random

295   intercept and random slope on ID would be included. If individual differences in the intercept

296   only were reported when testing H1, then the random intercept on ID would be included (and

297   not the random slope). Finally, whether the within- and between-individual components of the

298   climatic variables differed from each other was assessed by looking if the estimate (β_B - β_W) is

299   close to zero and statistically non-significant (see the method in van de Pol & Wright, 2009).

300   Following the procedure that we recently presented (Paoli et al., 2018), we reported the

301   averaged estimates of the coefficients of parameters in the base models, following the model

302   averaging approach (Schielzeth, 2010; Symonds & Moussalli, 2011) and using the model.avg

303   function in the R package AICcmodavg (Mazerolle 2017, <www.r-project.org>). The variables

304   included in the models were considered important if their 95% CIs excluded 0.

305   Females attributes early in life and between-individual heterogeneity in mean calving date and

306   in phenotypic plasticity (H3)

307   To evaluate the hypothesis that conditions early in life would shape female lifetime

308   phenotypic value (i.e. calving date) or females' plastic response to climatic changes (i.e.

309   individual slopes), we tested the interaction term between each of the female attribute and the

310   within-individual component (β_W) of the climatic variables in independent models, similar to

311   the   following   as   an   example: $Calving\ date \sim \text{T°May}_{within} + \text{T°May}_{between} +$

312    $\text{PrecApril}_{between} + \text{BD} * \text{PrecApril}_{within} + (1|\text{Year})$

313   The interaction term was tested in each of the base models and then model-averaged. If a

314   statistically significant between-individual heterogeneity in slopes was precedently found, then

315   we would focus on the interaction term with the climatic variable for which the reaction norms

316   differ between individuals (e.g. PrecApril_within). This method applied on the base models would

317   allow to simply test if a certain female attribute (e.g. BD) would cause consistent differences in

318   intercept and eventually slopes among females in regard to their plastic response to climatic

319   variables. Given that the females' attributes had only one value per female and to avoid the

320   random intercept on ID to capture too much variability that we tried to explain by females'

321   attributes, we decided to remove the random intercept on ID from the models. Moreover, as our

322   hypothesis was focusing on the females' attributes trying to explain the inter-individual

323   differences in intercept and slope regarding climatic variability; we also removed the fixed-

324   effects of females' BCI and proportion of males from the models.

325   Fitness consequences of between-individual heterogeneity in mean calving date and in

326   phenotypic plasticity (H4)

327   We used the same method as above to test our fourth hypothesis that individual

328   differences in mean calving date or between-individual heterogeneity in phenotypic plasticity

329   could lead to fitness consequences later on. As such, we tested the interaction term between

330   attributes of fitness and the within-individual component (β_W) of the climatic variables, similar

331   to the   following   as   an   example: $Calving\ date \sim \text{T°May}_{within} + \text{T°May}_{between} +$

332    $\text{PrecApril}_{between} + \text{Calf birthweight} * \text{PrecApril}_{within} + (\text{PrecApril}_{within}|\text{ID}) + (1|\text{Year})$.

333   The interaction term was tested in each of the two base models and then model-averaged. To

334   focus on the inter-individual differences in intercept and slope regarding climatic variability

335   having potential fitness consequences, we also removed the fixed-effects of females' BCI and

proportion of males from the models. However, and given that one different fitness attribute value was available per calving date, we kept the random intercepts on ID and year.

Results

Applying the within-subject centering method on the three best-fitted models from Paoli et al. (2018), and with a reduced dataset of females who calved at least four times over their reproductive life, made the fit of the third base model to drop substantially, with a ΔAIC > 4 (Table 1). Only the two first base models were therefore kept in the subsequent analyses. A statistically significant repeatability was found for calving date (ICC = 0.19, 95% CI [0.15, 0.24]), with the within-female variation being higher than the among-female variation.

Individual differences in mean calving date and between-individual heterogeneity in phenotypic plasticity (H1)

The comparison of different random structures of our two base models revealed an increase of all models' fit when female ID was entered as a random factor (Table 2), indicating that females varied in their average calving date (i.e. intercept). The inclusion of a random effect of female identity on slopes for precipitation in April also significantly decreased the deviance of the models (Table 2). A negative correlation was found between intercepts and slopes ($r = -0.24$ in model 1 and $r = -0.25$ in model 2) such that females with earlier calving dates in the average climate were more likely to delay their calving dates in response to the amount of precipitation in April. On the contrary, females with later calving dates advanced their calving dates with an increasing *PrecApril*. The best random structure of all models therefore appeared to be with a random intercept on female ID and with a random slope for *PrecApril* (Table 2), confirming scenario 2 of phenotypic plasticity described in the introduction (Fig. S1b). Both the fixed and random effects of those models explained between 44% and 45% of the variation in calving date, with 65% of the total variance explained by the residuals. For the random

360 effects, 15% of the total variance was explained by the random intercept on year, 18% by the

361 random intercept on ID and only 2% by the random slope of ID on PrecApril_within.

362 *Within- and between-individual response of calving date to climatic variability*

363 *(H2)*

364 The averaged fixed-effect estimates of our two models with their respective best random

365 structure (see Table 2) showed a population-, as well as an individual-level trend of earlier

366 calving dates following warmer temperatures in May (Table 3; Fig. 2a). An individual-level

367 trend of earlier calving dates with warmer temperatures in April-May was also found but with

368 non-statistically significant population trend (Table 3; Fig. 2b). Based on the method described

369 by van de Pol and Wright (2009), the individual- and population-level trends were statistically

370 similar and going in the same direction for both T°May and T°April-May (respectively β_B - β_W

371 = -0.58, 95% CI [-1.96, 0.72] and β_B - β_W = -0.20, 95% CI [-1.44, 0.95]). As such, the phenotypic

372 plasticity of calving date to T°May corresponded to scenario 1 in Fig. 1a, while the plastic

373 response to T°April-May corresponded to scenario 3 (Fig. 1c). An individual-trend of earlier

374 calving dates following a decreasing amount of precipitation in April was also found (Table 3,

375 Fig. 2c). However, the individual plastic responses were not reflected at the population level

376 since the individual- and population-level trends for *PrecApril* were statistically different and

377 going in the opposite direction (respectively β_B - β_W = -1.80, 95% CI [-3.37, -0.24] in model 1

378 and β_B - β_W = -1.56, 95% CI [-3.07, -0.04] in model 2). At the population-level, delayed calving

379 dates were observed with less precipitation in April but the trend was not statistically significant

380 (β_B component in Table 3). The plastic response of calving date to *PrecApril* clearly

381 corresponded to scenario 3 in Fig. 1c. We also consistently found earlier calving dates with

382 females in better physical condition the year preceding calving (Table 3) and in years with a

383 higher proportion of males present in the herd the preceding mating season (Table 3).

Females attributes early in life and between-individual heterogeneity in mean

calving date and in phenotypic plasticity (H3)

386   A total of 22 models were performed, 11 models for each of the base model, with 2 base

387   models kept, and corresponding to the 11 females attributes early in life. Among the 11 females'

388   attributes used to test our last hypothesis, three were found to influence the females' intercept

389   but none influenced their plastic response to precipitation in April. Females will have

390   consistently earlier calving dates in the average climate throughout their reproductive life (i.e.

391   lower intercepts) when (1) their birthdate ('BD') was earlier ($b = 0.98$, 95% CI [0.65, 1.32], N

392      $= 1,611$, Fig. 3b), (2) their averaged physical condition from March to May before their first

393   calving season ('COND_FST_CALF') was higher ($b = -0.48$, 95% CI [-0.84, -0.11], $N = 1,333$,

394   Fig. 3b) and (3) their first calving date ('BD_FST_CALF') was earlier ($b = 1.51$, 95% CI [1.19,

395   1.82], $N = 1,688$, Fig. 3c). Females with a higher physical condition in March-April-May before

396   their first calving season will also have an earlier BD_FST_CALF ($b = -0.38$, 95% CI [-0.37, -

397   0.29]).

Fitness consequences of between-individual heterogeneity in mean calving date

and in phenotypic plasticity (H4)

400   A total of 6 models were performed, 3 models for each of the base model, with 2 base

401   models kept, and corresponding to the 3 fitness attributes of females. In terms of fitness

402   consequences, females with earlier calving dates throughout their reproductive life (i.e. lower

403   intercepts) had heavier calves ($b = -0.94$, 95% CI [-1.26, -0.62], $N = 1,750$, Fig. 4a), calves with

404   a higher first-summer survival ($b = -0.80$, 95% CI [-1.11, -0.50], $N = 1,733$, Fig. 4b) and an

405   overall higher number of calves ($b = -0.70$, 95% CI [-1.02, -0.37], $N = 1,764$, Fig. 4c). Females

406   with a negative plastic response to *PrecApril* (i.e. I×E < 0) also had an overall higher number

407   of calves over their reproductive life ($b = -0.48$, 95% CI [-0.79, -0.16], $N = 1,764$, Fig. 5).

Discussion

Individual differences in mean calving date and between-individual heterogeneity in phenotypic plasticity

Our 45 years-long dataset of calving season allowed to demonstrate that the magnitude of the plastic response of calving date to a reduced amount of precipitation in April (mainly snowfalls at this time of the year) did vary among females (Table 2). Females also differed markedly in their mean calving date, confirming a between-individual heterogeneity in plasticity. The between-individual heterogeneity in maternal plasticity of birth timing has already been investigated in a number of animal species [birds: Bourret et al. 2015; Brommer, Pietiäinen, & Kolunen, 2003; Brommer, Rattiste, & Wilson, 2008; Przybylo et al. 2000; mammals: review in Boutin & Lane 2014], but so far this is the first study to demonstrate that in *Rangifer*. In addition, repeatability in calving date appeared to be quite low compared to birds, where the repeatability of laying date range between 0.10 and 0.61 (Potti, 1999; Wiggins, 1991). In mammals, a repeatability ranging from 0.54 to 0.93 was found in roe deer (Plard et al., 2013) and a repeatability of 0.10 in red deer (Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006). A repeatability of 0.19 thus suggests a high level of plasticity for calving date in this population. As expected, the large intraspecific differences in body mass of females reported in this herd (see Fig. 1 in Paoli et al., 2018), resulted in a between-individual heterogeneity in plasticity. In reindeer, large between-individual heterogeneity in females' body weight is mainly due to variations in food acquisition resulting from social dominance such that high-ranked females have access to the best food patches (Skogland, 1983, 1989). Given that calving date is highly determined by a female's physical condition (Barboza & Parker, 2008; Cameron et al., 1993; Cook et al., 2004; Flydal & Reimers, 2002), it resulted in females with a better overall physical condition being the ones calving earlier (Table 3). The high plasticity

432   reported in calving date would thus be accounted for by the among-females large variability in

433   body weight.

434   That Nussey et al. (2006) found a similarly low repeatability and that the magnitude of

435   phenotypic plasticity between calving date and autumn rainfall did vary among hinds in their

436   wild red deer population study (Nussey, Clutton-Brock, et al., 2005) points out that wild and

437   domesticated populations of ungulate species may respond to climate change in an individual-

438   specific manner. However, the variation in individual slope (IxE) in our study accounted for

439   2% of the total variance, while it accounted for 5.1% in the study of Nussey, Clutton-Brock, et

440   al. (2005) and the between-individual heterogeneity in intercept was much higher in our study

441   (18% versus 9.6% in Nussey, Clutton-Brock, et al., 2005). It suggests that management

442   practices could act to reduce the between-individual heterogeneity in slopes (i.e. reduce IxE),

443   although the individual, genetic variation in calving date is present (Nussey et al., 2007) and

444   higher than in red deer. Management practices are directed towards optimizing meat production

445   through the slaughtering of calves (Kumpula, Colpaert, & Nieminen, 1998). Given the

446   economic aspect of reindeer husbandry, reindeer herders are less likely to keep females with a

447   physical condition below the threshold to be able to reproduce in the herd. The supplemental

448   feeding given to the animals in late winter would cause females with a very low physical

449   condition to not be represented in this population, which may not be the case for wild

450   populations. Therefore, while supplemental feeding was unable to buffer completely the effects

451   of climatic variability on calving season (see Paoli et al., 2018) and to counteract the high

452   among-females heterogeneity of plasticity in calving date, it could have contributed to

453   homogenize the plastic responses of females to the amount of precipitation in April.

454   *Within- and between-individual response of calving date to climatic variability*

455   An individual-level trend of earlier calving dates following warmer temperatures in May

456   and in April-May was found using this reduced dataset of multiparous females (Figure 2a, b

19

457   and Table 3). Combined with the absence of a statistically significant variation in individual

458   slope (Table 2), it suggests that all females were able to respond to warmer temperatures in May

459   and in April-May by adjusting their calving date in the same way. However, a slight difference

460   among individual slopes was found for the amount of precipitation in April (Fig. 2c and Table

461   2), with a statistically significant individual response as well (Table 3). Those findings

462   confirmed that the precedent observed population-level correlations between calving date and

463   climatic variability (in Paoli et al., 2018) were driven by phenotypically plastic responses at the

464   individual-level. The supplemental feeding by sustaining the females' body weight above a

465   certain threshold might have helped females to be physiologically able to respond in a similar

466   manner to climatic conditions in spring. The mediated effect of the amount of precipitation in

467   April on females' physiological condition would, however, result in more heterogeneity in their

468   plastic responses. The explanation as to why the amount of precipitation creates a higher

469   among-females heterogeneity in phenotypic plasticity than the temperature is uncertain.

470   Perhaps a higher amount of precipitation in April leads to a greater climatic deterioration in

471   comparison to the mean temperature in May or in April-May, resulting in reduced food

472   availability for individual females. The social dominance in reindeer with high-ranked females

473   having access to the best food patches by digging under the snow (Skogland, 1983, 1989) would

474   then slightly accentuates the among-females differences in physical condition when the climate

475   deteriorates (i.e. more snowfalls).

476   At the population-level, earlier calving dates were reported in environments with warmer

477   temperatures in May (Fig. 2a and Table 3), while the between-individual effect in response to

478   precipitation in April was not statistically significant (Fig. 2c and Table 3). This might arise

479   because the absence of a statistically significant temporal trend for the amount of precipitation

480   in April (95% CI [-0.05, 0.08]) would lead the average climate between females to be quite

481   similar. On the contrary, significantly warmer temperatures in May ($b = 0.03$, 95% CI [0.03,

482   0.04]) over the past 45 years have contributed to produce more heterogeneous climatic

483   conditions between females, that have in turn influenced the between-female effect. This result

484   therefore demonstrates that a non-statistically significant population trend (scenario 3 in Table

485   S1 and Fig. 1c) does not necessarily mean that individuals will not be able to track their

486   changing climate by altering the expression of a phenotypic trait such as calving date. On the

487   contrary, an absence of an individual-level trend does not mean that the population lacks

488   plasticity of a particular trait to be able to respond to climatic variability and a population-level

489   trend might still be reported because certain phenotypes occur more frequently with certain

490   climatic conditions (scenario 2 in Table S1 and Fig. 1b). More emphasis should be put into

491   differentiating individual- from population-level analyses of phenotypic plasticity for such

492   reason. If the amount of precipitation in April was to change more in the future, however, more

493   heterogeneous climatic conditions between females, along with the inter-individual differences

494   in phenotypic plasticity could cause some females to be maladapted. As such, variability in

495   plasticity if genetically-based would then be under selective pressures (Brommer et al., 2005;

496   Coulson, Kruuk, Tavecchia, Pemberton, & Clutton-Brock, 2003; Nussey, Postma, et al., 2005;

497   Réale et al., 2003) to favour females better adapted to ongoing climatic changes in Finnish

498   Lapland, favoring the resilience of reindeer populations to climate change.

499   *Females attributes early in life and between-individual heterogeneity in mean*

500   *calving date and in phenotypic plasticity*

501   The majority of studies on phenotypic plasticity investigated whether or not being plastic

502   conferred a selective advantage (Brommer et al., 2003; Lane, Kruuk, Charmantier, Murie, &

503   Dobson, 2012; Nussey, Clutton-Brock, et al., 2005) or even if such plasticity was under

504   selection pressure (Brommer et al., 2005; Coulson et al., 2003; Nussey, Postma, et al., 2005;

505   Réale et al., 2003). However, most of these studies have not assessed how conditions

506   experienced early in life could explain a between-individual heterogeneity in the average

phenotype or in phenotypic plasticity (except Nussey, Clutton-Brock, et al., 2005). Unexpectedly, the different plastic responses to the amount of precipitation in April were not shaped by a female's physiological condition (95% CI [-0.32, 0.44]; contrary to Nussey, Clutton-Brock, et al., 2005; Bårdsen et al. 2008; Stopher, Pemberton, Clutton-Brock, & Coulson, 2008) or by any of the females attributes early in life tested in this study. However, and as commonly observed in ungulate species, we found a variation in mean calving date among females. Females born later than the population average and that also conceived later at their first calving event will begin their reproductive life at a disadvantage since giving birth consistently later throughout their reproductive life (Fig. 3b, d). As previously shown in ungulate species, late-born calves are disadvantaged, as summer forage quality becomes increasingly low and they are also provided with less time to grow before their first winter (Cook et al., 2004; Côté & Festa-Bianchet, 2001; Festa-Bianchet, 1988). On the contrary, their early-born counterparts have a "head-start" benefit via an accelerated growth, and this "head-start" advantage is maintained throughout lifetime (Cook et al., 2004; Feder, Martin, Festa-Bianchet, Bérubé, & Jorgenson, 2008).

As previously reported (see Aikio & Kojola, 2014; Kumpula & Colpaert, 2003; Paoli et al., 2018), the early spring period appeared a key period for the reproductive success of reindeer as females with a higher physical condition in spring before their first calving season will have an earlier first calving date and thereafter earlier calving dates throughout their lifetime (Fig. 3c). A better physical condition during the last trimester of pregnancy certainly contributed to advance the date at which the foetus is mature, resulting in an earlier birth (Rowell & Shipka, 2009). Based on our previous results (Paoli et al., 2018), we believe that phenotypic plasticity in gestation length (Clements, Clutton-Brock, Albon, Pemberton, & Kruuk, 2011; Mysterud et al., 2009) allowed calving date to be fine-tuned by proximate cues such as climatic conditions in late pregnancy through a mediated effect on the maternal nutrition and physiological state

532 (Barboza & Parker, 2008; Ropstad, 2000; Rowell & Shipka, 2009). These findings thus indicate

533 that a female's starting point when facing climatic changes is best predicted by her own

534 phenotypic quality at birth and all the way up to her first calving event, supporting the

535 importance of maternal-offspring inheritance of genetic and phenotypic components

536 (Muuttoranta, Holand, Røed, Tapio, & Nieminen, 2013; Weladji et al., 2006). It also supports

537 the assumption that differences among individuals early in life may contribute to consistent

538 differences in phenotypic value (e.g. mean calving date) observed later on (Nussey, Clutton-

539 Brock, et al., 2005; Stamps, 2016). However, the different individual plastic responses to the

540 amount of precipitation in April were not 'pre-determined' by any of the females attributes

541 early in life tested in this study. One possible explanation would be that the supplemental

542 feeding has hampered the expression of more heterogeneous individual trajectories in regard to

543 climate change (only 2% of the total variation was explained by the variation in individual

544 slope). Alternatively, another unidentified factor could be responsible in determining females'

545 different trajectories. Indeed, the trajectories between females greatly differed, with slopes to

546 the amount of precipitation in April ranging from -1.79 to 1.78. Other sources of variation might

547 be involved, such as 'permanent environment', maternal and indirect genetic effects (Brommer

548 et al., 2008; Dingemanse, Kazem, Réale, & Wright, 2010). Individual differences in slope might

549 be caused by an individual-specific exposure to a combination of climatic conditions

550 permanently affecting a female's plasticity (permanent environment: 'PE' in Dingemanse et al.,

551 2010). We speculate that negative or positive within-individual association between calving

552 date and the amount of precipitation in April might mask trade-offs made at the individual-level

553 between the amount of precipitation in April and a combination of other climatic variables.

554 Understanding the genetic or climatic causes of between-individual heterogeneity in plasticity

555 therefore remains very intricate. As pointed out, empirical support for studies enlightening

556   whether plasticity can vary (or not) as a function of experiences early in life is currently sparse

557   and equivocal (Stamps, 2016) but our study will be added to this expanding body of literature.

558   *Fitness consequences of between-individual heterogeneity in mean calving date*

559   *and in phenotypic plasticity*

560   In terms of fitness consequences, the females who had a negative plastic response to the

561   amount of precipitation in April (i.e. advanced their calving dates) gave birth to more calves

562   over their reproductive life (Fig. 5). It could suggest that females physiologically able to

563   advance their calving dates, despite a higher amount of precipitation in April, could benefit

564   from a high-quality forage at an earlier stage of lactation (Festa-Bianchet, 1988), even if more

565   precipitation in April might cause the onset of spring green-up to be delayed (Pettorelli,

566   Pelletier, von Hardenberg, Festa-Bianchet, & Côté, 2007). In turn, females feeding on the

567   longest possible highest-quality vegetation period (in early spring) could provide their calves

568   with a protein-rich milk and provide greater maternal care being in a high enough body

569   condition to invest towards reproduction (Barboza & Parker, 2008; Parker, Barboza, & Michael,

570   2009). Even if the reported effect size is quite small (see Fig. 5), it however points out that if

571   climatic changes were to exacerbate with more precipitation in April, inter-individual

572   differences in the number of calves produced might become greater and a positive plastic

573   response to the amount of precipitation in April might occur.

574   A lower intercept also conferred a reproductive advantage since females with consistently

575   earlier calving dates gave birth to heavier calves (Fig. 4a), calves with a higher first-summer

576   survival (Fig. 4b) and to more calves over their reproductive life (Fig. 4c), as found in other

577   studies (Brommer et al., 2003; Nussey, Clutton-Brock, et al., 2005; Réale et al., 2003).

578   Unfortunately, approximately one third of the calves are slaughtered every fall as a management

579   practice, therefore we could not estimate long-term fitness consequences on this population. A

580   recent study on roe deer revealed that a higher allocation to reproduction early in life led to an

24

impaired performance later in life with long-term fitness consequences (Lemaître et al., 2018) and an apparent direct fitness benefit of plasticity was found in a wild red deer population with females more plastic to dry autumns having a higher number of calves that survived to 2 years of age (Nussey, Clutton-Brock, et al., 2005). Generally, these results corroborate the assertion that climatic conditions experienced while *in utero* and early in life can determine an individual's phenotypic value and phenotypic plasticity and therefore shape the adult lifetime reproductive success as commonly observed in ungulate species (Forchhammer et al., 2001; Kruuk et al., 1999; Post & Stenseth, 1999). However, the underlying physiological mechanisms on why such conditions early in life are able to determine the average phenotype later in life or the average phenotypic plasticity remain unclear. In most ungulate species, a general trend of earlier calving dates following better climatic conditions has been reported (Moyes et al., 2011; Nussey, Clutton-Brock, et al., 2005; Post & Forchhammer, 2008) but whether the females differed in the magnitude of their plastic response has received contrasted responses. Our results therefore emphasize the need to better understand the underlying mechanisms leading to the complexity of plastic responses among populations to cope with current climate change (Boutin & Lane, 2014).

Authors' contributions statement

AP, RBW and ØH conceived the project, AP analysed the data with input from RBW. AP wrote the manuscript with input from RBW, ØH and JK.

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Figures
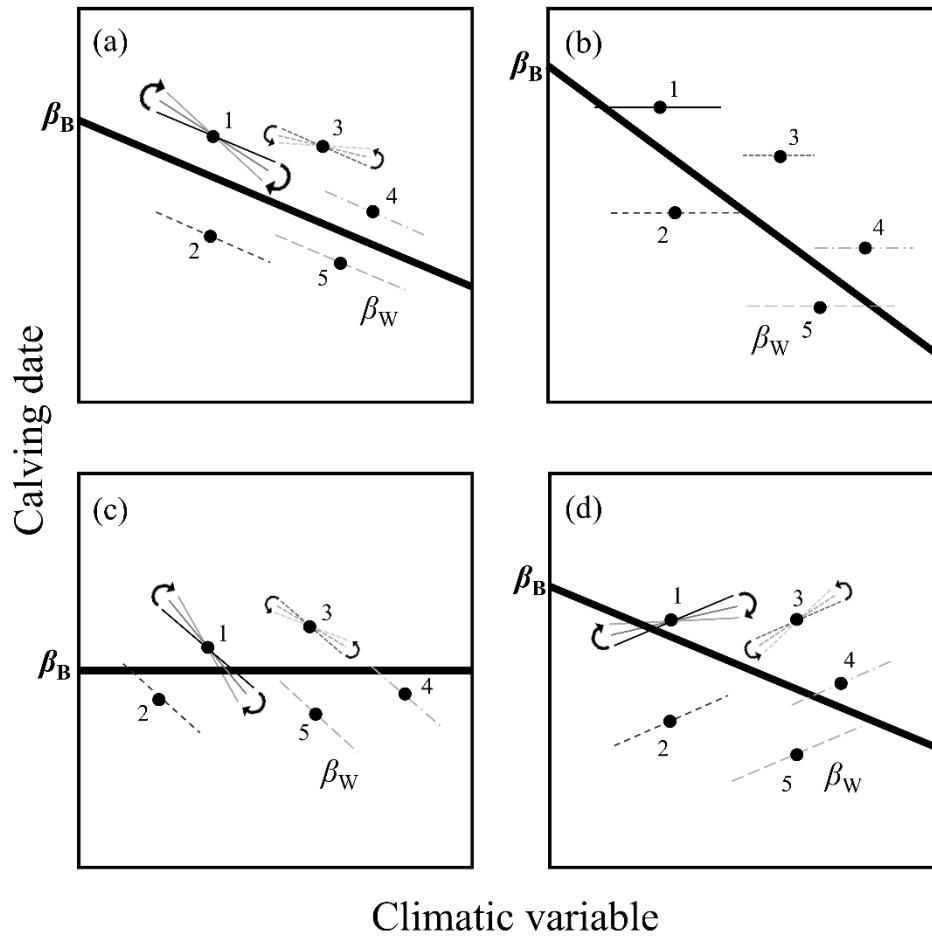
Fig. 1. Four different scenarios for how within- and between-individual plastic responses of calving date to a climatic variable can differ (or not) in a population. The between-individual slope was schematically represented with a thick solid line (β_B), depicting the population trend. The within-individual slopes were represented for five different females (1 to 5) with thin lines (β_W). Each black dot (•) was the mean calving date of a female on the y-axis and the average climatic conditions that she has experienced over her lifetime on the x-axis, while the line represented her plastic response of calving date to climatic variability. The slopes between females could differ such that female 1 could have a negative slope, while female 3 could have a positive slope, as represented by the lighter slopes and the arrow showing the direction of the change
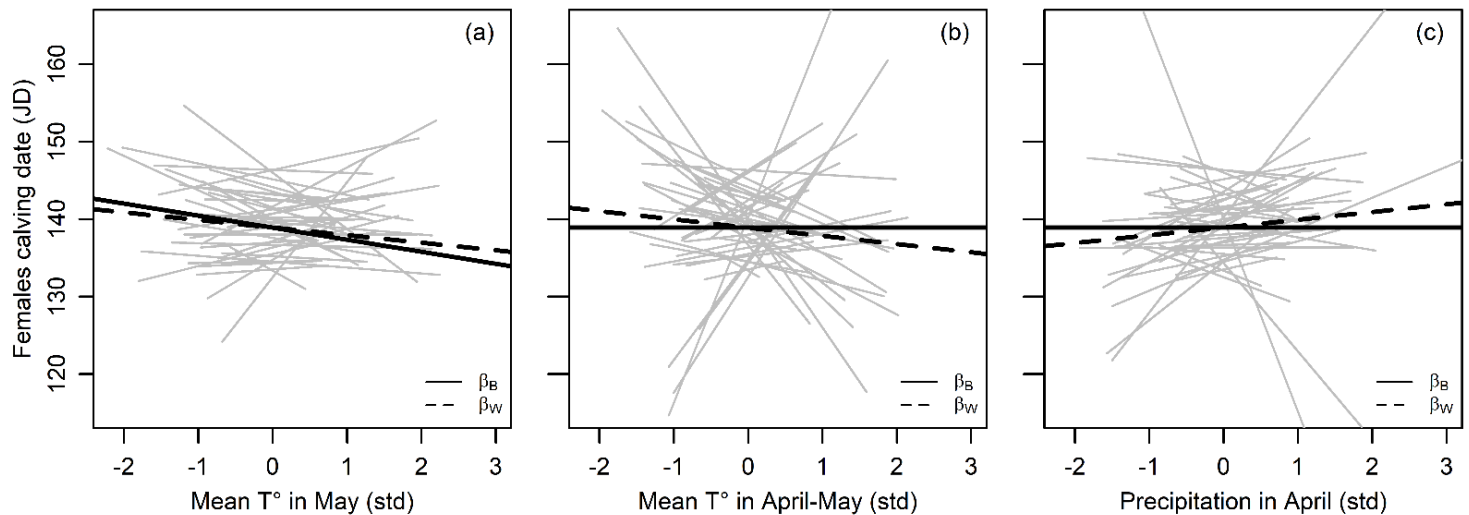
820   **Fig. 2.** Individual-specific plasticity of calving date (in Julian days) for 50 randomly chosen

821   reindeer females (from a total of 272 females) of the Kutuharju herd to (a) mean temperature in

822   May, (b) mean temperature in April-May and (c) amount of precipitation in April. The grey

823   lines represent the model-averaged individual estimates for intercept and slope, obtained by

824   running linear regression models of calving date against (1) mean temperature in May and the

825   amount of precipitation in April for model 1 and (2) mean temperature in April-May and the

826   amount of precipitation in April for model 2, separately for each female. Following the subject-

827   centering method, the climatic variables were subdivided into a within- (β_W) and a between-

828   individual component (β_B). The bold, straight black lines represent the average population-level

829   plastic response (β_B) of calving date to the climatic variable of interest, while the bold, dotted

830   black lines represent the individual-level trend (β_W). The population- and individual-level

831   trends were obtained from the model-averaged estimates in Table 3
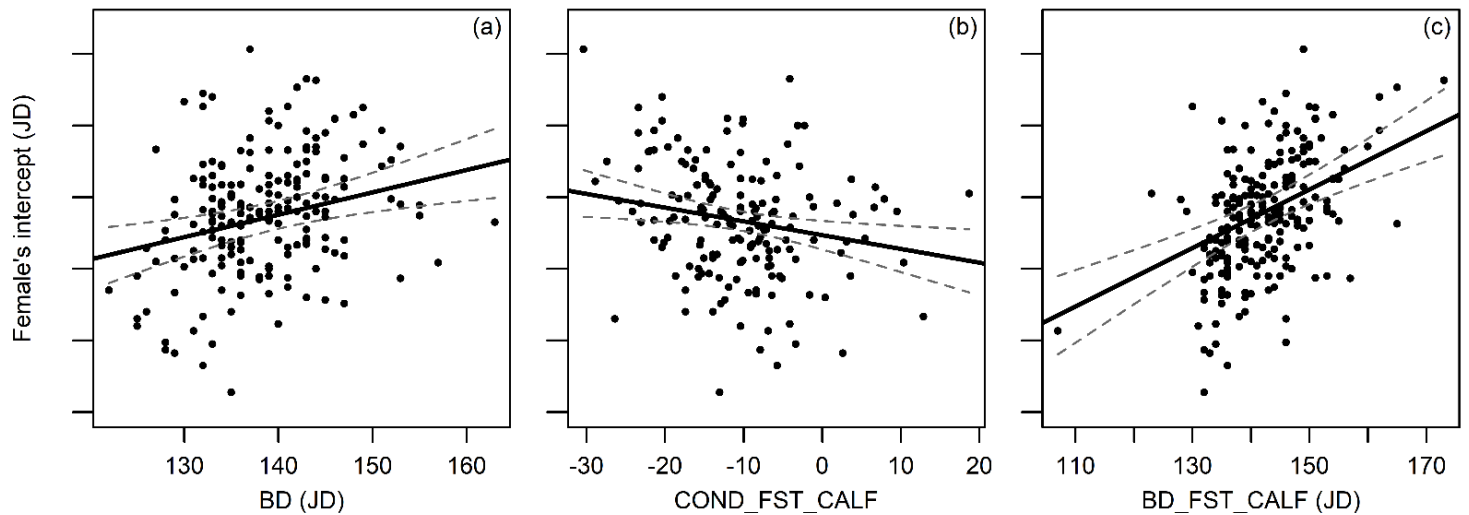
832 **Fig. 3.** The between-individual heterogeneity in intercept of calving date in response to climatic

833 variability from a semi-domesticated reindeer population in Kaamanen, northern Finland was

834 influenced by (a) the birthdate of the female of interest ('BD'), (b) the average physical

835 condition of the female in March-April-May before her first calving season

836 ('COND_FST_CALF') and (c) her first calving date ('BD_FST_CALF'). BD and

837 BD_FST_CALF were expressed in Julian days. Each dot (●) represented the model-averaged

838 female's intercept from individually independent regression fits of calving date against (1)

839 mean temperature in May and the amount of precipitation in April for model 1 and (2) mean

840 temperature in April-May and the amount of precipitation in April for model 2. Following the

841 subject-centering method, the climatic variables were subdivided into a within- (β_W) and a

842 between-individual component (β_B)
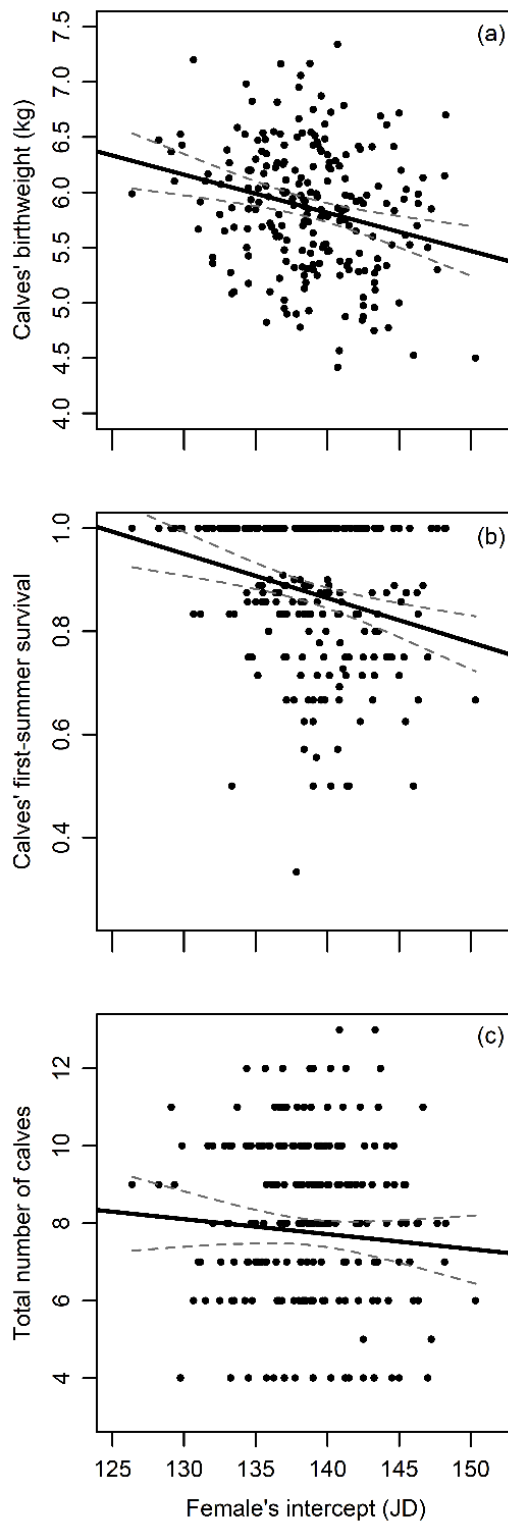
843   **Fig. 4.** The between-individual heterogeneity in intercept of calving date in response to climatic

844   variability from a reindeer population in Kaamanen, northern Finland and its consequences on

845   (a) the calves' birthweight, (b) the calves' first-summer survival and (c) the total number of

846   calves of a female. Each dot (●) represented the model-averaged female's intercept from

847   individually independent regression fits of calving date against (1) mean temperature in May

848   and the amount of precipitation in April for model 1 and (2) mean temperature in April-May

849   and the amount of precipitation in April for model 2. Following the subject-centering method,

850   the climatic variables were subdivided into a within- (β_W) and a between-individual component

851   (β_B)
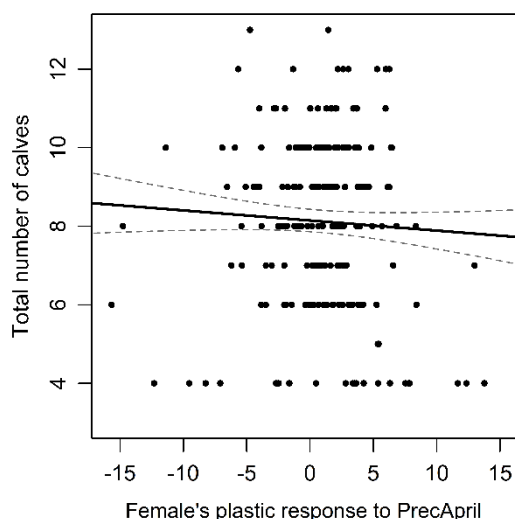
Fig. 5. The between-individual heterogeneity in the plastic response of calving date to the amount of precipitation in April ('PrecApril') of the females in the Kutuharju herd, northern Finland and its consequences on the total number of calves of a female. Each dot (●) represented the model-averaged female's slope to the amount of precipitation in April from individually independent regression fits of calving date against (1) mean temperature in May and the amount of precipitation in April for model 1 and (2) mean temperature in April-May and the amount of precipitation in April for model 2. Following the subject-centering method, the climatic variables were subdivided into a within- (β_W) and a between-individual component (β_B)

Table 1. Competing linear mixed-effects models for calving date of a reindeer population in Kaamanen, northern Finland in relation to climatic variability. From Paoli et al. (2018), the same climatic variables were used (mean temperature in May 'T°May'; mean temperature in April-May 'T°April-May'; the amount of precipitation in April 'PrecApril' and the snow depth index in April 'SDIApril') but with a reduced dataset of females who calved at least four times over their lifetime ($N = 1,770$ calving dates from 272 different females). All models included female identity and year as random factors, as well as females' body condition index (BCI) and proportion of males in the herd (PM) as fixed effects. A within-individual centring technique was applied as suggested by van de Pol and Wright (2009) to distinguish between population- ($\beta_{B, \text{'between'}}$) and individual-level ($\beta_{W, \text{'within'}}$) trends (see text for details)

Rank	Models	AICc	*df*	AICc weights	ΔAICc
1	BCI + PM + T°May$_{within}$ + T°May$_{between}$ + PrecApril$_{within}$ + PrecApril$_{between}$	11533.8	10	0.61	0.0
2	BCI + PM + T°April-May$_{within}$ + T°April-May$_{between}$ + PrecApril$_{within}$ + PrecApril$_{between}$	11535.1	10	0.32	1.3
3	BCI + PM + T°May$_{within}$ + T°May$_{between}$ + SDIApril$_{within}$ + SDIApril$_{between}$	11538.0	10	0.07	4.2

868

869 **Table 2.** Comparison of linear mixed-effects models of calving date to climatic variables in the Kutuharju area, northern Finland with different

870 random structures and showing deviance estimates and log-likelihood ratio test (LRT) statistics. The number for the set of models indicates which

871 one of the base models was used (see Table 1). Random slopes were regressed with the within-individual component (β_W, 'within') of climatic

872 variables. The models in bold text appeared to be the models with the best random structure in explaining variation in calving date

Set of models	Models	Log-L	Deviance	df	Test	LRT	P-value
1	0. Year	-5822.3	11645				
	1. Year + ID	-5756.8	11514	1	0 vs. 1	131	< 0.001
	2. Year + ID × T°May$_{within}$	-5755.2	11510	2	1 vs. 2	3.23	0.20
	3. Year + ID × PrecApril$_{within}$	**-5753.4**	**11507**	**2**	**1 vs. 3**	**6.78**	**0.03**
2	0. Year	-5823.6	11647				
	1. Year + ID	-5757.5	11515	1	0 vs. 1	132	< 0.001
	2. Year + ID × T°April-May$_{within}$	-5757.5	11515	2	1 vs. 2	0.07	0.96
	3. Year + ID × PrecApril$_{within}$	**-5754.0**	**11508**	**2**	**1 vs. 3**	**6.96**	**0.03**

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874 **Table 3.** Model-averaged estimates of fixed effects from the linear mixed-effects models of calving date of a reindeer population in relation to

875 climatic variables in Kaamanen, northern Finland, produced from a dataset of females who calved more than four times (272 mothers), between

876 1970 and 2016. The estimates were subdivided into a within-individual component ($\beta_{W,\text{ 'within'}}$) and a between-individual component ($\beta_{B,\text{ 'between'}}$) as

877 suggested by van de Pol and Wright (2009) (see text for details) and those in bold type were deemed important (whose 95% CI excluded 0) in

878 explaining calving date. "Nbr models" is the number of models (out of the two best models in Table 1) including that variable

Variable	Estimate	Unconditional SE	Nbr models	Relative importance	95% CI
Females' BCI	**-1.24**	0.22	2	1.00	**-1.68, -0.80**
Proportion of males	**-1.50**	0.32	2	1.00	**-2.12, -0.87**
PrecApril$_{\text{within}}$	**1.00**	0.44	2	1.00	**0.14, 1.86**
PrecApril$_{\text{between}}$	-0.71	0.85			-2.38, 0.95
T°May$_{\text{within}}$	**-0.98**	0.45	1	0.63	**-1.85, -0.10**
T°May$_{\text{between}}$	**-1.55**	0.72			**-2.96, -0.15**
T°April-May$_{\text{within}}$	**-1.06**	0.50	1	0.37	**-2.05, -0.08**
T°April-May$_{\text{between}}$	-1.27	0.66			-2.57, 0.03

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