



# Phenotypic plasticity in bighorn sheep reproductive phenology: from individual to population

Limoilou-Amelie Renaud<sup>1,2</sup> · Gabriel Pigeon<sup>1,3</sup> · Marco Festa-Bianchet<sup>1,2</sup> · Fanie Pelletier<sup>1,2</sup>

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## Abstract

Climate change can lead to a mismatch between resource availability and key life history events. Without plasticity in reproductive traits, that mismatch can lower fitness and decrease population size. In birds, phenotypic plasticity is frequently reported as the main mechanism to track environmental changes, but evidence for plasticity in large mammals is scarce. Using long-term individual-based data, we quantified phenotypic plasticity in 394 parturition dates of 137 bighorn sheep ewes (average 2.9 per ewe, range 1–11 parturition dates) in response to environmental drivers. Over 26 years, we detected a population response to environmental drivers, as median parturition date advanced by 15 days. Our study area showed temporal trends in population density, precipitation in October–November and temperature in August–November. Increasing autumn precipitation was associated with later parturition. Increasing autumn temperature was associated with earlier parturition but the effect was weak. Analyses of the between- and within-individual components of weather, climate and density revealed an individual adjustment to autumn precipitation. We detected no plasticity in response to variation in temperature and density and no variation in plasticity (no  $I \times E$ ) in response to any determinants of parturition date. Our results suggest that the reproductive phenology of species with long and fixed gestation may respond more to environmental drivers in autumn than in spring.

## Significance statement

Many organisms time reproductive events based on seasonal availability of food resources. Climate change, however, can affect the timing of food availability. Organisms can change the timing of reproduction over the short term through phenotypic plasticity. Little is known, however, about how much individual plasticity in reproductive timing exists in wild mammals. We examined phenotypic plasticity in parturition date in bighorn sheep in response to changes in autumn precipitation, autumn temperature, a global climate index and adult female density. Temporal trends in these variables over 26 years partly explained a 15-day advance in average parturition date. Individual ewes only appeared to show plasticity in response to autumn precipitation, suggesting some capacity to cope with rapid global environmental changes over the short term.

**Keywords** Climate change · Large vertebrate · Parturition date · Phenotypic plasticity · Precipitation · Temperature

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✉ Limoilou-Amelie Renaud  
limoilou.renaud@gmail.com; limoilou-  
amelie.renaud@usherbrooke.ca

<sup>1</sup> Département de Biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada

<sup>2</sup> Centre d'Études Nordiques, Université Laval & Centre de la science de la biodiversité du Québec, McGill University, Stewart Biology Building, Montreal, QC, Canada

<sup>3</sup> Environmental science and nature management, Norwegian University of Life Sciences, Universitetstunet 3, 1433 Ås, Norway

## Introduction

Rapidly changing climate presents organisms with the challenge of synchronizing reproductive phenology with temporally shifting availability of seasonal resources (Parmesan 2006). Phenological traits are especially sensitive to rapid environmental changes because even slight mismatches in timing, for example of parturition or laying date, can compromise juvenile survival (Both et al. 2009; Ozgul et al. 2010). By altering the timing of phenological events, particularly the onset of spring in temperate and boreal environments, changes in climate modify the temporal windows to which organisms must synchronize reproduction. Although some species respond by changing reproductive timing, including parturition date (Ozgul et al. 2010; Moyes et al. 2011), negative fitness consequences of phenological mismatch have been reported, such as delayed emergence of hibernators leading to inability to accumulate sufficient fat before the next hibernation (Lane et al. 2012). Synchrony of reproductive traits and resource availability is important for demography because it may affect offspring growth and survival (Ozgul et al. 2010; Plard et al. 2014), especially in environments with a short season when high-quality food resources are available (Visser et al. 2012).

Organisms can adapt to climate change either through phenotypic plasticity (Charmantier et al. 2008; Porlier et al. 2012) or microevolution (Boutin and Lane 2014; Merilä and Hendry 2014). For example, individual phenotypic plasticity allows great tits (*Parus major*) to adjust laying date in response to increasing spring temperature without microevolution, enabling the population to closely track a rapidly changing environment (Charmantier and Gienapp 2014). Phenotypic plasticity is generally accepted as the main mechanism to cope with short-term changes in the environment, especially in birds (reviewed in Gienapp et al. 2008), but microevolution may be required over a longer time scale if changes increase in magnitude (Boutin and Lane 2014).

One challenge in measuring phenotypic plasticity is establishing which environmental predictors are most likely to affect phenology (van de Pol et al. 2016). Both climate-related indices, such as ocean warming (Gibbin et al. 2017) and local weather variables such as mean temperature (Bourret et al. 2015) and precipitation (Hogg et al. 2017; Siepielski et al. 2017) have been used to investigate phenotypic plasticity as well as adaptations (Siepielski et al. 2017). The ecological drivers of plastic traits, however, remain unknown for most mammals. Even when environmental cues can be linked to plastic variation in traits, mechanisms underlying trait responses often remain unclear (Uller et al. 2013; Forsman 2015).

Demographic parameters can also influence the expression of phenotypic plasticity in reproductive traits. In moose (*Alces alces*), population density, winter climate and age affect the timing of conception (Veeroja et al. 2013). Density-

dependence in timing of reproduction can be driven by changes in body condition caused by competition for resources (Mysterud et al. 2008), but density effects are not always consistent. Following changes in temperature, female swallows (*Tachycineta bicolor*) expressed less phenotypic plasticity in laying date at low than at high density (Bourret et al. 2015), likely because low density was associated with less suitable habitat. Red squirrels (*Tamiasciurus hudsonicus*), on the other hand, are territorial and breeder density is related to competition for resources (Dantzer et al. 2013). High density leads to increased maternal glucocorticoids in gestating females. Increased hormonal concentrations, here a plastic trait, are transmitted to offspring to ‘prepare’ for the expected future environment; this hormonal increase leads to higher growth rate in young squirrels through maternal phenotypic plasticity (Dantzer et al. 2013). Multiple ecological variables can have synergetic effects on phenological traits, complexifying the choice of relevant environmental variables at the population and individual levels.

Both environmental and maternal conditions during the rut affect parturition date in bighorn sheep (*Ovis canadensis*) at the population level (Feder et al. 2008), but it remains unknown if individuals show variability in plastic responses to environmental changes. The first objective of this study was to investigate environmental drivers of variation in parturition date in bighorn sheep at the population level. Bighorn sheep show very little flexibility in gestation length ( $\bar{x} \pm SD = 172.7 \pm 2.1$  days; Hogg et al. 2017); we thus hypothesized that phenological changes near the time of conception the previous autumn would affect parturition date. Changes in parturition date could be explained by changes in weather and climate variables or in population density, or both. Density sharply decreased during our study, potentially relaxing competition for forage and favouring earlier parturition (Festa-Bianchet 1988a; Pigeon et al. 2017). In parallel, our study area experienced a substantial increase in autumn temperature and a decrease in precipitation. Increasing autumn temperatures, combined with dry conditions, may be followed by rapidly shifting plant phenology and seasonal availabilities of food resources (Post and Stenseth 1999) – perhaps extending the season of plant growth and therefore improving female condition during autumn. We therefore expected that higher temperatures and higher precipitation in autumn would respectively advance and delay parturition date at the population level. In the study population, high density is associated with later parturition date (Rioux-Paquette et al. 2011) but whether individuals show variation in their plastic response to density is unknown. We expected that increasing density (number of females aged  $\geq 2$  years) at conception would delay parturition because of density-dependent competition for resources.

Our second objective was to identify the drivers of individual-level phenotypic plasticity in parturition date. To quantify individual differences in parturition date, we

calculated repeatability of parturition date using linear-mixed effects models (Nakagawa and Schielzeth 2010). Plasticity can be approximated as the ‘reverse’ of repeatability (1-R; Nakagawa and Schielzeth 2010). Repeatability can be low for two reasons: high within-individual (residual) variation or low between-individual variation. In our study, repeated measurements of parturition date were taken in different environments (years); environmental and ‘individual-by-environment interaction’ (or  $I \times E$ ; Nussey et al. 2007) variance components contribute to the residual variance and, thus, to 1-R (Nakagawa and Schielzeth 2010). Despite potential between-individual differences in parturition date, we expected repeatability to be low because of high residual variance, leaving high potential for phenotypic plasticity in parturition date. Thus, we hypothesized that the population response to weather, climate and density was driven by individual plasticity. Distinguishing between average population responses from individual-level phenotypic plasticity can provide important insights on whether or not long-lived animals can express rapid responses to environmental changes. Individuals may also differ in their degree of plasticity ( $I \times E$ ; Nussey et al. 2007). We thus quantified variation in individual plasticity in parturition date. We used long-term data from a wild population of bighorn sheep in Alberta, Canada, with repeated measurements of individuals from birth to death. We first quantified temporal trends in average parturition date over 26 years and the influence of environmental and demographic variables at the population level using a linear mixed model framework. We then used mean-centering (van de Pol and Wright 2009) to investigate plastic responses to ecological variables.

## Methods

### Study area and data collection

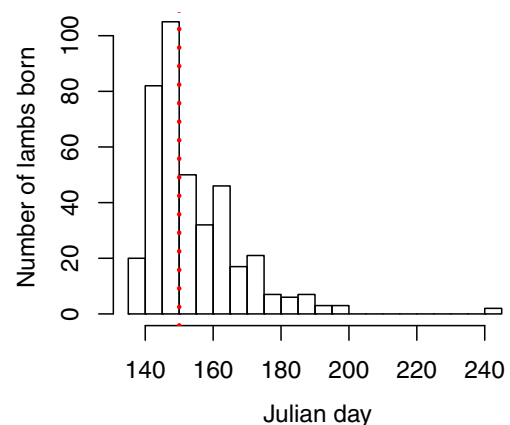
The Ram Mountain bighorn sheep population is located in Alberta, Canada (52° N, 115° W, elevation 1080–2170 m). Since 1971, sheep have been captured in a corral trap baited with salt and monitored daily from late May to late September. Parturition date was estimated from 1992 to 2017 (except for 1993) by a combination of behavioural and morphological observations, including lamb size, presence of the umbilical cord and dark grey coat (Geist 1971). Ewes isolate themselves for 2–3 days post-partum with their lambs before they join other ewes (Festa-Bianchet 1988b). Numbers of days since the ewe was last seen before giving birth allowed us to estimate age of lambs and to backtrack their birthdate. We recorded parturition date in Julian day starting 1 January. Weaning is in late September (Festa-Bianchet 1988b). To meet normality assumptions, we log-transformed parturition date starting with Julian day 136 as day 0 (i.e. the earliest estimated parturition

date; Fig. 1). Behavioural observations during lactation and molecular analyses confirmed mother–young associations. Since our study involved marked animals in the field, it was not possible to record data blind.

Of all lambs that survived to mid-September, 98% were marked in their first summer (see Jorgenson et al. 1993 for details on sampling design). From 1992 to 2017, 137 females gave birth at least once (average 2.9 times, range 1–11 parturition dates). We have at least two estimations of parturition dates for 91 ewes that were included in plasticity analyses. Mass, age and reproductive status were available for all these females. We adjusted female mass (kg) for capture date using linear mixed-effects models with restricted maximum likelihood where both the intercept and the slope were allowed to vary for each individual (Martin and Pelletier 2011). Female mass adjusted to 15 September was treated as a continuous variable. ‘Maternal mass in September’ in analyses is this adjusted mass in September prior to parturition. We defined yearly reproductive success as a three-level factor variable: ‘did not reproduce’ ( $n = 82$  female-years), ‘did not wean a lamb’ ( $n = 123$ ) and ‘weaned a lamb’ ( $n = 194$ ).

### Environmental and demographic variables

Precipitation (total rainfall plus water equivalent of snowfall in mm per day) and mean daily temperature (°C) were obtained from the Environment Canada meteorological station at Nordegg, about 20 km west of Ram Mountain. A sliding window was used to determine the relevant period over which to calculate average temperature and precipitation, using ‘slidingwin’ function from the R library ‘climwin’ (Bailey and van de Pol 2016). Most conceptions are in late November–early December (Hogg 1984; Hogg et al. 2017). As bighorn sheep show very little flexibility in gestation length (Hogg et al. 2017), we assumed that conception occurred 172 days before parturition. Therefore, we considered



**Fig. 1** Bighorn lambs born each Julian day at Ram Mountain, Alberta, Canada, 1992 to 2017. The median birthdate of May 30th is indicated by a vertical dotted line (non-leap year)

all possible windows of all possible lengths between the earliest parturition date (16 May) and the earliest predicted conception date (26 November). We used windows based on the same starting and ending dates for all individuals (an ‘absolute’ sliding window; Bailey and van de Pol 2016). We selected the window that provided the lowest AIC for models of log-transformed parturition date over the weather and climate variables being tested. Precipitation was thus averaged from 21 October to 15 November (AIC lower than model without precipitation by 22.16) while mean daily temperatures were averaged from 30 August to 19 November (AIC lower than model without temperature by 21.52) in the conception year. Total precipitation and mean daily temperatures are referred to as autumn precipitation and autumn temperature. Pacific Decadal Oscillation (PDO) values were available each year from 1992 (<http://jisao.washington.edu/pdo>). The PDO, similarly to the North Atlantic Oscillation, is a global climate index characterized by a 10-year cycle of alternating cold and warm phases in Western North America. It is measured as the leading principal component of North Pacific monthly sea surface temperature variability (Mantua et al. 1997). Monthly values were averaged over the months of July and August prior to parturition (‘summer PDO’) based on a sliding window (AIC lower than model without PDO by 1.12). Population size (referred to as density) is quantified each year in June as the number of females aged 2 years and older (Pigeon et al. 2017). We used density in June in the year of conception to analyse parturition date. Density mostly declined after 1992 (Fig. 2a).

### Temporal trends and determinants of parturition date at the population level

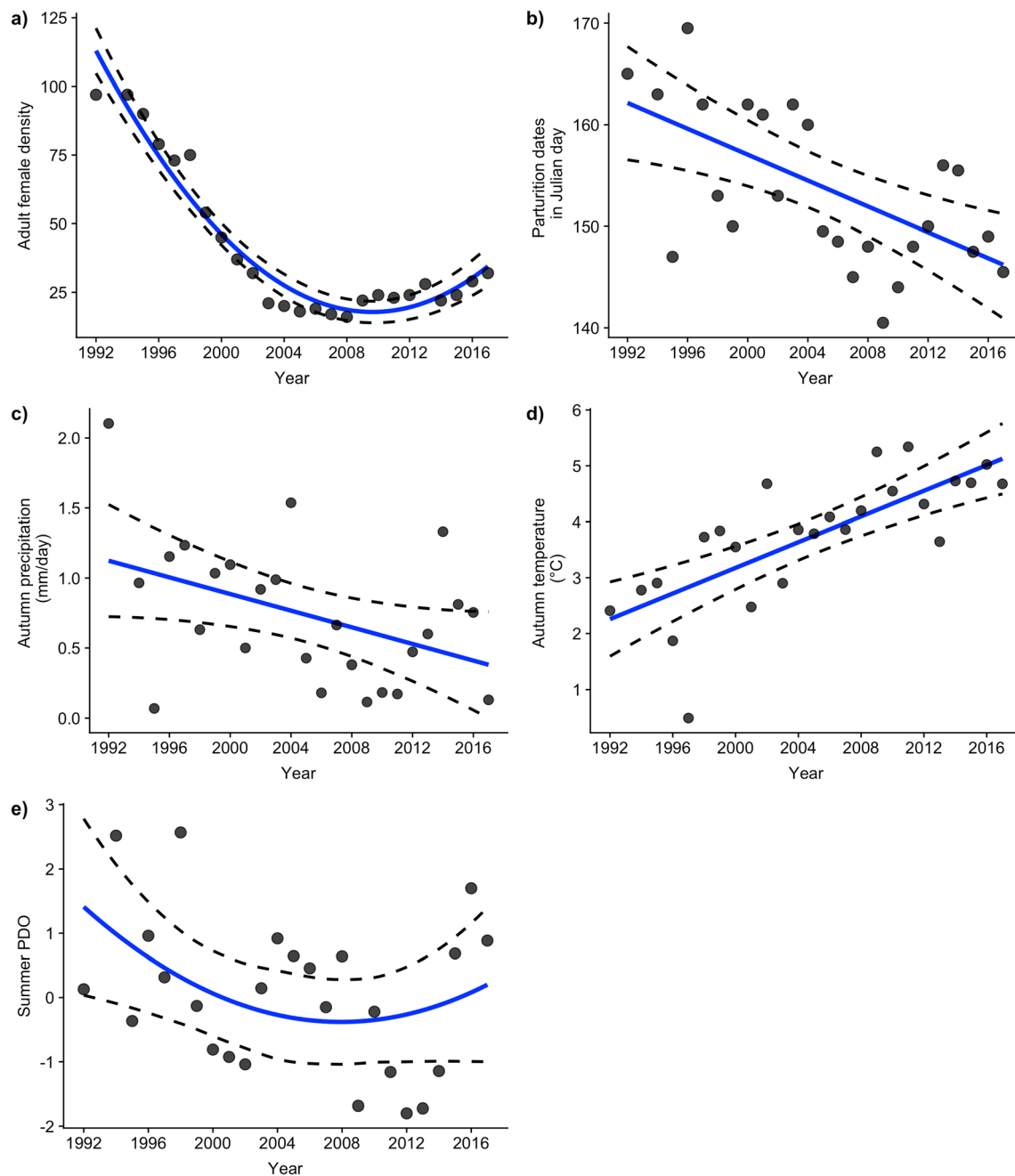
We used general linear models with a Gaussian error distribution to estimate annual trends in median parturition date ( $r = 0.90$  between median and mean parturition dates), with year, autumn precipitation, autumn temperature, density and summer PDO fitted as continuous variables over the 26 years of study. To avoid spurious correlations, we removed the temporal effects from summer PDO, autumn precipitation, autumn temperature and density. Density and summer PDO were expressed as the residuals of a linear regression over year as a quadratic variable, while autumn temperatures and precipitation were expressed as the residuals of a linear regression over year. These variables are hereafter referred to as ‘detrended’ (Grosbois et al. 2008). We used linear mixed-effects models to test the effect of detrended precipitation, temperature and PDO as linear and quadratic terms on log-transformed parturition date, and their two-way interactions with detrended density. We conducted separate analyses for each predictor to avoid model over-fitting. Final models for each set of variables were determined by sequentially removing the least significant term from the model based on its  $P$

value. Significance of model terms was then assessed with likelihood ratio tests (LRTs; difference in log-likelihood between hierarchical models, tested against a chi-square distribution with the number of degrees of freedom that corresponded to the difference in the number of terms estimated). Our baseline model included maternal mass in September and previous reproductive success as fixed effects (Feder et al. 2008). All other models added one variable to the baseline model. Year and female identity were included as random effects in analyses of the effects of environmental determinants on log-transformed parturition date to account for pseudo-replication and unexplained annual variation in parturition date.

We then calculated repeatability from the baseline model, with and without year as a random effect, to measure how much of between- or within-individual differences could be attributed to year-to-year variation in parturition date. Repeatability is the amount of phenotypic variation that can be attributed to between-individual variation over the sum of between- and within-individual variations (Nakagawa and Schielzeth 2010). The non-repeatable fraction of phenotypic variation should thus correspond to the sum of measurement error and individual phenotypic plasticity. In the absence of significant between-individual variation in slopes ( $I \times E$ ), the variance attributable to individual identity will remain constant across all values of an environmental covariate and can be used to estimate the repeatability of a trait. We provide estimates and 95% confidence intervals calculated by parametric bootstrapping in R package ‘rptR’ (Nakagawa and Schielzeth 2010).

### Phenotypic plasticity

To quantify within-individual plastic responses of parturition date to environmental variation, we used random regression models. All environmental variables were standardized to zero mean and unit variance (see values prior to standardisation, Table S1 in Supplementary Online Material). Given the lack of quadratic effects of autumn precipitation, autumn temperature, summer PDO and density at the population level, only their linear effects were tested at the individual level. To facilitate interpretation, we repeated plasticity analyses with both raw and detrended predictors. Estimates from the models fitted on detrended predictors are in the Supplementary Online Material. Maternal mass in September and previous reproductive success were included in our baseline model. Within-individual plastic responses can also be quantified using within-subject mean centering (van de Pol and Wright 2009). Within-subject centering decomposes environmental effects into those associated with the average environment experienced by each individual over its lifetime (a ‘between-individual’ effect) and those attributable to yearly deviations of the environment from each individual’s lifetime average



**Fig. 2** Temporal trends at the population level in **a** adult female density, **b** median parturition date, **c** autumn precipitation (mm/day), **d** autumn temperature ( $^{\circ}\text{C}$ ) and **e** summer PDO at Ram Mountain, Alberta,

Canada, 1992 to 2017. All predictors were measured during the year of conception, previous to parturition, up to 2016. Grey circles represent annual values and lines are model predictions (dotted lines: 95% CI)

(the ‘within-subject’ effect). Within-subject centering considers that individuals experience different ranges of environmental conditions over their lifetime and centering around subjects’ means eliminates any between-subject variation. Each environmental covariate was thus subdivided into a within-individual ( $\beta_{\text{W}}$ ) and a between-individual ( $\beta_{\text{B}}$ ) component, by subtracting the individual’s mean value (the  $\beta_{\text{B}}$ , reflecting the population trend) from each individual observation ( $x_{ij} - \bar{x}_j$ , or  $\beta_{\text{W}}$ , reflecting plasticity). Following van de Pol and Wright (2009), we modelled parturition date ( $y_{ij}$ ) for each

individual  $i$  in year  $j$  as a continuous response to variation in each of the weather, climate or density variables. For example, the model for precipitation was as follows:

$$y_{ij} = \beta_0 + \beta_{\text{B}} \bar{\text{Prec}}_i + \beta_{\text{W}} (\text{Prec}_{ij} - \bar{\text{Prec}}_j) + \text{mass} + \text{prs} \\ + [\text{year}] + [\text{ID}_i] + [\text{ID}_i (\text{Prec}_{ij} - \bar{\text{Prec}}_j)] + e_{0ij}$$

where  $\beta_0$  represents the intercept and, as the predictors (here precipitation) were standardized to zero mean, is equivalent to the expected parturition date in the average environment. The

between-subject effect ( $\beta_B$ ) is estimated as the slope of  $y_{ij}$  on the mean value of each predictor for each individual,  $i$ . The within-subject ( $\beta_W$ ) effect is estimated as the slope of  $y_{ij}$  on the annual deviation of the predictor from the subject mean. ‘Mass’ and ‘prs’ refer to maternal mass the previous autumn and previous reproductive success, while  $e_{ij}$  represents the residual error.

The presence of within-individual plasticity in the population could thus be investigated using within-subject mean centering, while variation in within-individual plasticity ( $I \times E$ ) was investigated using random regression models (Nussey et al. 2007). The random effects are shown in square brackets in the previous equation:  $[ID_i]$  quantifies the variation in within-subject intercepts, and  $[ID_i (\text{Prec}_{ij} - \bar{\text{Prec}}_i)]$  quantifies the variation in the within-subject slopes for the effects of precipitation (Nussey et al. 2007). Year was included as a random effect to model variation across years that were not explained by environmental variables. We ran similar models for autumn temperature, summer PDO and female density. LRTs revealed that the random slope effects of the environmental variables were not significant (Table 1). We thus kept the random intercepts of identity and year in further analyses and in visual representations of individual plastic responses to precipitation and temperature. We included females with more than one parturition date to quantify their response to environment and to improve uncertainty estimates around within-

individual slopes ( $n = 350$  observations of 91 females out of 442 total observations, average of 3.85 parturition dates per female). All linear mixed models were computed using R library ‘lme4’ and function ‘lmer’ (Bates et al. 2015). We calculated a pseudo- $R^2_{\text{marginal}}$  for fixed effects and a pseudo- $R^2_{\text{conditional}}$  combining fixed and random effects according to Nakagawa and Schielzeth (2013). We performed all analysis on R version 3.5.1 (R Core Team 2018).

## Results

### Determinants of parturition date at the population level

Most births in 1992–2017 occurred in late spring (median date: May 30, mean date  $\pm$  SD: June 3  $\pm$  12.4 days), with 80% of lambs born in the 27 days after May 16th (Fig. 1). Median parturition date advanced by approximately 15.7 days over 26 years ( $\beta = -0.63$  [ $-0.98$  to  $-0.27$ ],  $\text{adj-}R^2 = 0.34$ ; Fig. 2b). During this time, the number of adult females decreased from 103 to 37 ( $\beta_{\text{Year}} = -1231$  [ $-1466.54$  to  $-995.14$ ],  $\beta_{\text{Year}}^2 = 0.31$  [ $0.25$ – $0.37$ ],  $\text{adj-}R^2 = 0.94$ ; Fig. 2a). Density declined from 1992 to 2003, then stabilized and slightly increased, partly because of translocation of new individuals in 2003–2015 (Poirier and Festa-Bianchet 2018).

**Table 1** Random regression analyses to assess variation in plasticity, i.e. an individual-by-environment ( $I \times E$ ) component, in bighorn sheep parturition date ( $n = 350$ ), 1992 to 2017, Ram Mountain, Alberta, Canada. Three models with an increasingly complex random structure were compared for each of the four environmental variables: autumn precipitation, temperature, adult female density and summer PDO. Random structures of models 1 to 3, 4 to 6, 7 to 9 and 10 to 12 were compared with a LTR. All models included the within-individual ( $\beta_W$ )

and the between-individual ( $\beta_B$ ) components of the environmental variable as fixed predictors and maternal mass in September and previous reproductive success as control variables. Within-individual centering was applied as suggested by van de Pol and Wright (2009). Results from random regressions on ‘detrended’ predictors are found in Table S3, and estimates of models with  $I \times E$  are presented in Table S5 of the Supplementary Online Material

	Log-likelihood	Test	df	LRT	P
<b>Precipitation</b>					
1. Year	−285.33	–	8	–	–
2. Year + Female	−281.91	1 vs 2	9	6.86	0.009
3. Year + Female $\times$ Precipitation <sub>within</sub>	−281.22	2 vs 3	11	1.37	0.50
<b>Temperature</b>					
4. Year	−287.42	–	8	–	–
5. Year + Female	−284.74	4 vs 5	9	5.36	0.02
6. Year + Female $\times$ Temperature <sub>within</sub>	−283.40	5 vs 6	11	2.67	0.26
<b>Density</b>					
7. Year	−293.32	–	8	–	–
8. Year + Female	−289.62	7 vs 8	9	7.40	0.007
9. Year + Female $\times$ Density <sub>within</sub>	−289.59	8 vs 9	11	0.07	0.97
<b>Summer PDO</b>					
10. Year	−296.46	–	8	–	–
11. Year + Female	−293.03	10 vs 11	9	6.86	0.009
12. Year + Female $\times$ PDO <sub>within</sub>	−291.62	11 vs 12	11	2.83	0.24

Daily precipitation decreased by 0.7 mm over the study period ( $\beta_{\text{Year}} = -0.03$  [-0.06 to -0.003],  $\text{adj-}R^2 = 0.16$ ; Fig. 2c) and autumn temperature increased by 2.9 °C ( $\beta = 0.12$  [0.07–0.16],  $\text{adj-}R^2 = 0.54$ ) (Fig. 2d). There was no clear trend in summer PDO ( $\beta_{\text{Year}} = -28.32$  [-67.69 to 11.06],  $\beta_{\text{Year}}^2 = 0.01$  [0.00–0.02],  $\text{adj-}R^2 = 0.08$ ; Fig. 2e).

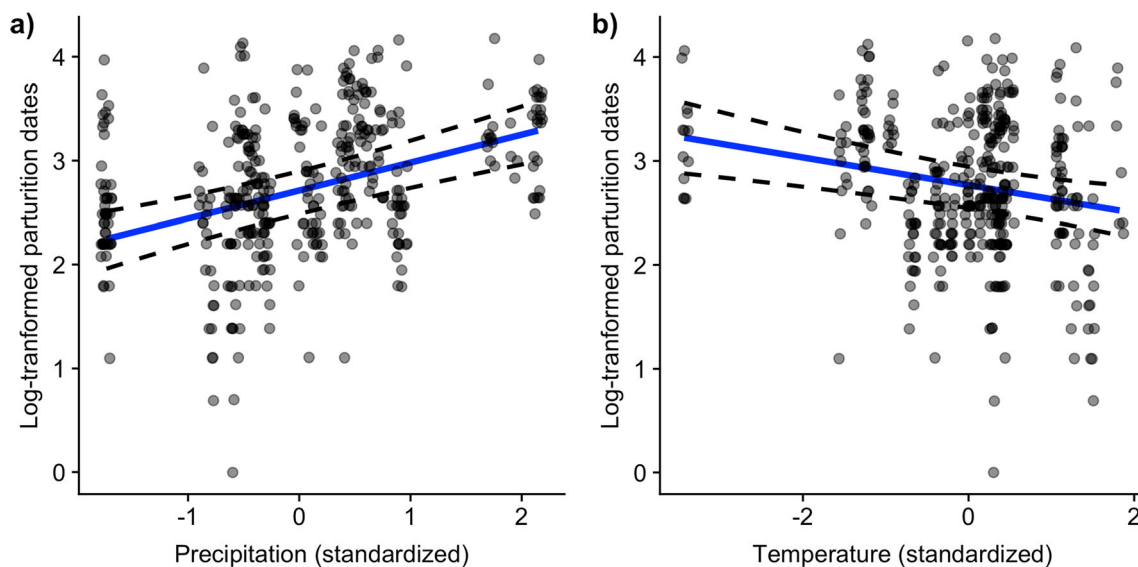
At the population level, all results include parameter estimates for detrended environmental and density variables. The final models for precipitation and temperature only included linear effects of precipitation and temperature (Fig. 3a, b; Table S2). Increasing precipitation was associated with a delay in parturition of  $\sim 17.3$  days over the study period (Fig. 3a; Table S2), but the effect of temperature was not significant. There was no significant effect of density, either as a linear or quadratic term or in interaction with climate or weather variables, on log-transformed parturition date. Effects of summer PDO were also negligible (Table S2). Reproductive success was treated as a three-level factor; relative to females that had not reproduced the previous year ( $\beta = 2.77$  [2.59–2.97]), females that weaned a lamb delayed parturition by  $\sim 1.3$  days ( $\beta = 2.85$  [2.69–3.00]) and those that lost their lamb during summer advanced parturition by  $\sim 2.0$  days ( $\beta = 2.63$  [2.47–2.79]; Fig. 4a). Heavier females gave birth slightly earlier: mass in September advanced parturition by  $\sim 7.6$  days over the observed range of standardized maternal mass ( $\beta = -0.10$  [-0.16 to -0.03]; Table S2; Fig. 4b).

After accounting for maternal mass in September and previous reproductive success, repeatability was weak but significant ( $R = 0.21$  [0.10–0.32]) suggesting that  $\sim 21\%$  of variation in parturition date was attributed to individual differences.

When year was included as a random effect, repeatability was reduced to 0.07 [0.01–0.15], suggesting that part of the between-individual differences in parturition date can be explained by year-to-year variations in the environment. Adding year decreased the residual variance ( $\text{Var}_{\text{residual}} = 0.25$  [0.20–0.29]), but whether or not year was included in the model, the ratio of residual variance to between-individual variance was high, suggesting a potential for phenotypic plasticity in response to changes in the environment.

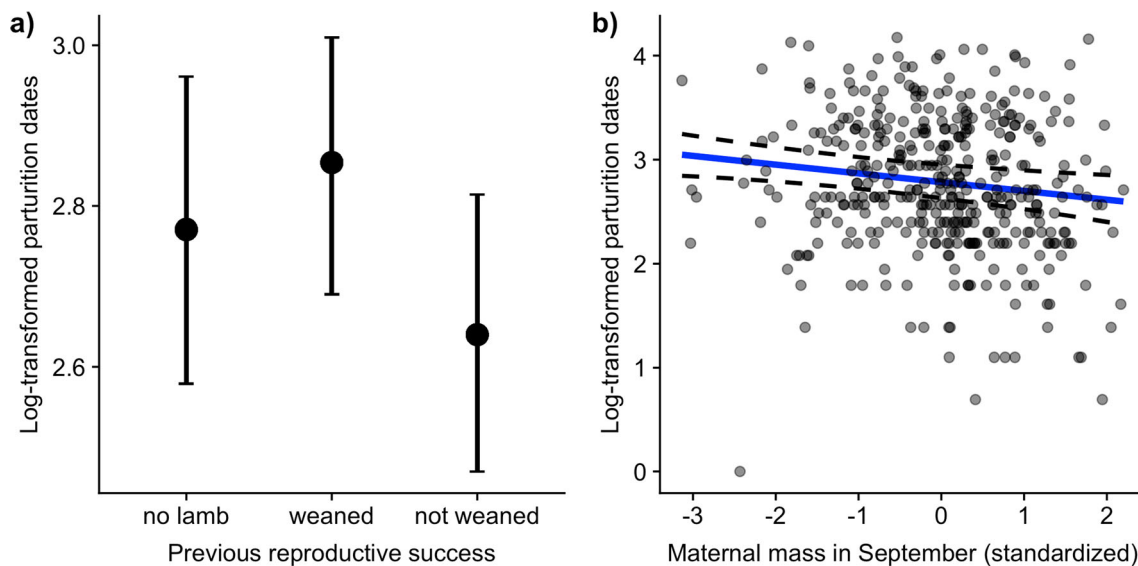
### Phenotypic plasticity in parturition date

Plasticity analyses included only linear effects of environmental variables. We present model estimates for random regressions and plasticity analyses fitted on raw predictors in the main text and in Tables 1 and 2. The equivalent models fitted on detrended predictors can be found in the Supplementary Online Material in Tables S3 and S4. We found significant individual plasticity in response to autumn precipitation ( $\beta_{\text{W}} = 0.28$  [0.16–0.40]) and to autumn temperature ( $\beta_{\text{W}} = -0.17$  [-0.32 to -0.01]), but not to adult female density ( $\beta_{\text{W}} = 0.04$  [-0.18 to 0.26] and summer PDO ( $\beta_{\text{W}} = 0.09$  [-0.08 to 0.26]; Table 2). Random regression analyses showed no variability of individual slopes of the relationships between environmental predictors and parturition date (no  $I \times E$  for precipitation, temperature, density or PDO) in the random part of models 3, 6, 9 and 12 in Table 1 (but see full model estimates with  $I \times E$  in Table S5). Variance in intercepts for female identity was 0.03 in all models (Table 2, random effects). Estimates for between-individual slopes showed effects for



**Fig. 3** Determinants of parturition date at the population level for bighorn sheep at Ram Mountain, Alberta, Canada, 1992 to 2017. Effects of **a** mean daily autumn precipitation ('detrended') and **b** mean autumn temperature ('detrended') on parturition date are illustrated. Parturition date was log-transformed starting at 0 on Julian day 136, the earliest recorded parturition. Previous reproductive success and

maternal mass in September were added as fixed effects (see Fig. 4), and female identity and year as random intercepts. Transparent, grey circles represent annual raw values. The blue line is a model prediction for a female of average mass that did not produce a lamb the previous year (dotted lines: 95% CI)



**Fig. 4** Effects of **a** previous reproductive success and **b** maternal mass in September on parturition date at the population level for bighorn sheep at Ram Mountain, Alberta, Canada, 1992 to 2017. Estimates are for a female of average mass in **a**. No lamb: no lamb produced the previous year; weaned: weaned a lamb the previous September; not weaned: lamb

produced the previous year died over the summer, including neonatal mortality. In **b**, transparent, grey circles represent annual raw values and the blue line is a model prediction for a female that did not produce a lamb the previous year (dotted lines: 95% CI). All estimates are from model 2 in Table 1

autumn precipitation ( $\beta_B = 0.43$  [0.26–0.60]) and temperature ( $\beta_B = -0.34$  [–0.49 to –0.20]; Fig. 5) and average density ( $\beta_B = 0.21$  [0.05–0.37]; Table 2). Effect of summer PDO ( $\beta_B = 0.09$  [–0.11 to 0.29]) was not significant. Results were similar when detrended predictors were used, except that within-individual plasticity in response to temperature was not significant (Tables S3 and S4).

In addition, we investigated whether heterogeneous sampling of individuals over the study period, with some females monitored only at low or high density, led to a spurious relationship of adult female density with log-transformed parturition date. Based on median density over the study period (median = 32, standardized value = –0.53), we separated years in two subgroups, low and high density, and repeated plasticity analyses for each subgroup. The between-individual density effect on parturition date was no longer significant ( $\beta_{B(\text{low})} = 0.03$  [–1.88 to 1.92],  $\beta_{B(\text{high})} = 0.17$  [–0.06 to 0.40]; Table S6), based on the model without  $I \times E$  in both subgroups.

Finally, if within-individual plasticity explains between-individual responses, their estimated slopes should be similar and  $\beta_B - \beta_W$  should be near zero and non-significant. We thus assessed whether within- and between-individual slopes were different by rewriting our initial model (e.g. precipitation) as follows:

$$y_{ij} = \beta_0 + (\beta_B - \beta_W) \text{Prec}_j + \beta_W (\text{Prec}_{ij}) + \text{mass} + \text{prs} \\ + [\text{year}] + [\text{ID}_i] + [\text{ID}_i (\text{Prec}_{ij} - \text{Prec}_j)] + e_{0ij}.$$

where the original fixed predictor effect ‘Prec<sub>ij</sub>’ now combines both within- and between-individual effects, and ‘Prec<sub>j</sub>’ only

expresses between-individual variation while controlling for within-individual effects. These analyses suggested a weak and non-significant difference between slopes for precipitation ( $\beta_B - \beta_W = 0.15$  [–0.02 to 0.32]), but the difference in slopes for temperature was significant ( $\beta_B - \beta_W = -0.18$  [–0.34 to –0.01], see equation 3 in van de Pol and Wright 2009 for more details on the method; Table S7). Detrended predictors gave slightly different results: the difference in slopes was not significant for precipitation ( $\beta_B - \beta_W = 0.03$  [–0.14 to 0.20]) but the difference in slopes for temperature was marginal ( $\beta_B - \beta_W = -0.08$  [–0.23 to 0.08]) and excluded the presence of plasticity in response to detrended temperature ( $\beta_W = -0.12$  [–0.27 to 0.03]; Table S4). Sample size influenced our capacity to detect plasticity. As the number of observations/female increased to 7 ( $n_{\text{females}} = 13$ ), between- and within-individual slope estimates increased in the model including adult female density ( $\beta_B = 0.84$  [–0.96 to 2.60]),  $\beta_W = 0.68$  [–0.17 to 1.58]; Fig. S1) but large confidence intervals and a large difference in slopes ( $\beta_B - \beta_W = 0.16$  [–1.58 to 1.89]) suggest that plasticity alone cannot account for all the observed population change. Increasing number of observations/female also increased the magnitude of the within-individual precipitation effect. In all models, however, sample size greatly decreased as number of observations/female increased from 2 ( $n_{\text{females}} = 91$ ) to 7 ( $n_{\text{females}} = 13$ ), resulting in wider confidence intervals (Fig. S1).

## Discussion

Mean parturition date in the study population now occurs 15 days earlier than 26 years ago. Our investigation of the



**Table 2** Parameter estimates of linear mixed-effects models of the effects of between-individual ( $\beta_B$ ) and within-individual ( $\beta_W$ ) components of (a) precipitation, (b) temperature, (c) adult female density and (d) summer PDO on 350 bighorn sheep parturition date, 1992 to 2017, Ram Mountain, Alberta, Canada. Estimates of fixed effects and variance components of random effects of models 2, 5, 8 and 11 are presented based on results in Table 1. Within-individual centering was applied as suggested by van de Pol and Wright (2009). PRS: reproductive success the previous year. Model estimates from ‘detrended’ predictors can be found in Table S4 and estimates of models with  $I \times E$  are presented in Table S5 of the Supplementary Online Material. Significant effects are in italics

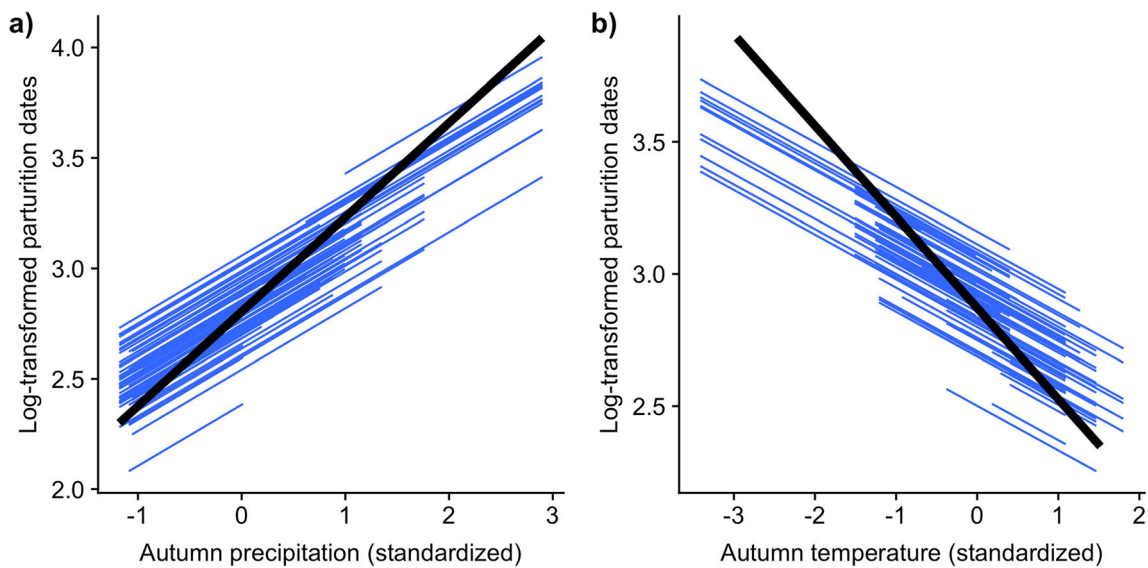
Fixed effects	Estimate	95% CI	Random effects	Variance
<b>(a) Autumn precipitation</b>				
Intercept (no lamb) ( $\beta_0$ )	2.80	2.62–2.99	Female (intercept)	0.03
Maternal mass	– 0.09	– 0.16 to – 0.02	Year (intercept)	0.06
PRS: not weaned	– 0.18	– 0.37 to 0.01	Residual	0.25
PRS: weaned	0.03	– 0.14 to 0.22	$R^2_{\text{marginal}}$	0.26
Precipitation <sub>between</sub> ( $\beta_B$ )	0.43	0.26–0.60	$R^2_{\text{conditional}}$	0.46
Precipitation <sub>within</sub> ( $\beta_W$ )	0.28	0.16–0.40		
<b>(b) Autumn temperature</b>				
Intercept (no lamb) ( $\beta_0$ )	2.87	2.67–3.07	Female (intercept)	0.03
Maternal mass	– 0.10	– 0.17 to – 0.03	Year (intercept)	0.09
PRS: not weaned	– 0.21	– 0.39 to – 0.01	Residual	0.25
PRS: weaned	0.01	– 0.17 to 0.19	$R^2_{\text{marginal}}$	0.22
Temperature <sub>between</sub> ( $\beta_B$ )	– 0.34	– 0.49 to – 0.20	$R^2_{\text{conditional}}$	0.46
Temperature <sub>within</sub> ( $\beta_W$ )	– 0.17	– 0.32 to – 0.01		
<b>(c) Female density</b>				
Intercept (no lamb) ( $\beta_0$ )	2.87	2.66–3.09	Female (intercept)	0.03
Maternal mass	– 0.09	– 0.17 to – 0.03	Year (intercept)	0.13
PRS: not weaned	– 0.20	– 0.39 to – 0.01	Residual	0.24
PRS: weaned	0.02	– 0.16 to 0.20	$R^2_{\text{marginal}}$	0.11
Density <sub>between</sub> ( $\beta_B$ )	0.21	0.05–0.37	$R^2_{\text{conditional}}$	0.46
Density <sub>within</sub> ( $\beta_W$ )	0.04	– 0.18 to 0.26		
<b>(d) Summer PDO</b>				
Intercept (no lamb) ( $\beta_0$ )	2.85	2.62–3.07	Female (intercept)	0.03
Maternal mass	– 0.09	– 0.16 to – 0.02	Year (intercept)	0.16
PRS: not weaned	– 0.19	– 0.37 to 0.01	Residual	0.25
PRS: weaned	0.04	– 0.14 to 0.22	$R^2_{\text{marginal}}$	0.05
PDO <sub>between</sub> ( $\beta_B$ )	0.09	– 0.11 to 0.29	$R^2_{\text{conditional}}$	0.47
PDO <sub>within</sub> ( $\beta_W$ )	0.09	– 0.08 to 0.26		

factors contributing to this change showed the importance of autumn precipitation and, to a lesser extent, autumn temperature. Our study area is experiencing a long-term increase in temperature and a decrease in precipitation (Douhard et al. 2017; this study), underpinning the need for bighorn sheep to track phenological changes. Individuals responded plastically to autumn precipitation, but not to autumn temperature, population density or summer PDO. We did not find evidence of individual differences in female capacity to adjust parturition date in response to environmental changes, as suggested by the absence of significant individual-by-precipitation or individual-by-temperature variability in our analyses. Our results suggest a rapid population response to changes in precipitation, likely due to a plastic response at the individual level rather than to evolutionary processes.

### Long-term changes in phenology

Female bighorn sheep advanced parturition date by about 0.63 day/year over the study period. This rate is higher than

the 0.42 day/year ( $\pm 0.08$  SE) advance in parturition date or the 0.26 day/year ( $\pm 0.07$  SE) advance in oestrus date reported in red deer in response to warming temperatures (Moyes et al. 2011; Stopher et al. 2014). Our analyses of the determinants of parturition date at the population level suggest that local weather, rather than large-scale climate indices or density, is more important for bighorn sheep reproductive phenology. We used a sliding window to determine the relevant period over which to quantify the effects of weather and climate variables on parturition date in the population. This window varied from July (PDO) to November (temperature and precipitation), thus covering late summer and autumn. Dry and warm autumns were associated with earlier parturition, suggesting earlier conception. Gestation length in bighorn sheep shows very little flexibility; therefore, conception date should be closely correlated with parturition date (Hogg et al. 2017), in contrast to other ungulates that show flexibility in gestation length (Clements et al. 2011). We thus hypothesize that mild autumns indirectly affect female body mass before conception through improved foraging conditions.



**Fig. 5** Effects of **a** mean daily autumn precipitation and **b** mean autumn temperature on parturition date for bighorn sheep at Ram Mountain, Alberta, Canada, 1992 to 2017. Parturition date was log-transformed starting at 0 on Julian day 136, the earliest recorded parturition. Previous reproductive success and maternal mass in September were added as fixed effects. Female identity and year were added as random intercepts (Table 1). Within-individual centering ( $\beta_B$  vs  $\beta_W$ ) was applied as

suggested by van de Pol and Wright (2009), and initial predictors (not ‘detrended’) were included in models. Thick, black lines represent the between-individual trend ( $\beta_B$ ), and thin, blue lines represent within-individual reaction norms ( $\beta_W$ ) obtained from predictions of linear-mixed effects models for a female of average mass that did not produce a lamb the previous year

Changes in parturition date could synchronize vital activities—such as lactation and subsequent conception—with changes in food abundance. Hogg et al. (2017) showed, in another bighorn sheep population, that females conceived earlier when summer and winter evapotranspiration, an index of food resources, increased. Seasonal precipitation improved body condition and advanced bighorn sheep parturition in their study area in Montana, at lower elevation and with a much drier climate than Ram Mountain. Mild autumn conditions could also favour earlier weaning of lambs, as reported in feral sheep (Forchhammer et al. 2001), and trigger early return to oestrus. Because most precipitation in late autumn falls as snow in our study area, and deep snow may decrease forage availability, one may expect high autumn precipitation to increase female energy expenditure and lower body condition, thus potentially delaying conception date (Feder et al. 2008).

Regardless of the mechanisms triggering conception in ewes and whether large-scale climate indices or local weather variables are measured, the association between parturition date and their determinants suggests that bighorn sheep can partly track phenological changes. Our results also highlight the importance of cues other than temperature (Thackeray et al. 2010; Siepielski et al. 2017) as drivers of reproductive phenology in ungulates. For example, latitude explains variation in birth season length (the number of days in which 80% of all births occur) in captive ruminants, supporting the hypothesis that photoperiod—although independent of climate change—has an important impact on ruminant reproduction (Zerbe et al. 2012).

We expected that increasing density would delay reproduction because of density-dependent competition for resources. Contrary to our prediction, there was no significant effect of density on parturition date. However, density effects remain difficult to assess due to potential time lags in population response. Finally, important within-individual variability led to low repeatability estimates of parturition date. Repeatability estimates of parturition date in bighorn sheep were lower than those measured in five populations of roe deer (range  $R = 0.54\text{--}0.93$ ), which are the highest reported for any mammal, suggesting low plasticity in this trait in that species (Plard et al. 2012). We thus suggest that intra-individual responses were expressed as phenotypic plasticity in response to environmental changes in bighorn sheep.

### Plasticity analyses of parturition date

Using linear mixed-effects models and mean-centering, we detected plasticity in parturition date in response to autumn precipitation. The difference in between- and within-individual slope estimates ( $\beta_B - \beta_W$ ) was near zero, suggesting that the population and individual responses are effectively the same and that individual plasticity (within-individual component,  $\beta_W$ ) may drive a population response to autumn precipitation. Autumn precipitation may be a cue for timing of reproduction in bighorn sheep. Whether this cue is related to changes in plant phenology or to other mechanisms is unknown, but patterns observed at the population and individual levels were very similar in direction and magnitude, strongly

suggesting that ewes adjust parturition date—through conception date—to changing environmental conditions. With climate change, earlier breeding may improve the match between parturition and optimal environmental conditions. Whether or not the phenotypic responses observed in this study are beneficial over the long term, however, will require further investigations of the consequences of plasticity on fitness in this population.

There was no plastic response to summer PDO or density, and the temperature effect disappeared when testing detrended temperature. The absence of effects, either at the population or individual level, does not seem to be entirely caused by an insufficient sample size. Increasing number of measurements per female increased the between-individual components of density, temperature and precipitation, but only the within-individual precipitation effect. Between- and within-individual density effects were not significant and had large confidence intervals resulting from small sample size. Summer PDO effects were independent of the number of observations/female. We finally investigated whether the between-individual density effect could be due to a heterogeneous sampling of individuals. Between- or within-individual density effects on parturition dates were not significant when analyses were restricted to either high or low density, or when density was detrended. Large differences in within- and between-individual slope estimates also suggest that plasticity did not explain the between-individual density effect when all females were included in analyses of ‘raw’ predictors. Altogether, these results suggest that a temporal trend in density or heterogeneous sampling of individuals explained a significant between-individual density effect and that plasticity could not explain this apparent response to density. Mechanisms for density effects in our study population thus remain unknown.

Finally, it is possible that other, unmeasured ecological variables drive plasticity in parturition date in bighorn sheep. However, our analyses are very conservative since we modelled year-to-year variations in parturition date that were not explained by environmental covariates, both at the population and individual levels, by including year as a random effect. Including year also accounted for multiple measures per year, which might lead to non-independent observations within years. Modelling this year-to-year variation possibly decreases the annual variability explained by covariates of interests such as precipitation, temperature, climate or density; however, the relatively high conditional coefficients of determination ( $R^2_c = 46\text{--}47\%$ ) suggest that our models effectively explained variation in parturition date while also excluding potential confounding temporal trends in covariates.

Rapid climate change occurs worldwide, and phenotypic plasticity may be key to population persistence. Shifting climates, particularly changes in precipitation patterns, present a challenge for many organisms (Siepielski et al. 2017).

Importantly, local and regional climate change may explain patterns of phenology much better than global change (Siepielski et al. 2017). For example, in our study, local precipitation was an important variable affecting parturition date. We found population- and individual-level changes, suggesting an effect of weather on the reproductive phenology of bighorn sheep. Variation in plasticity was very weak or could not be detected in response to changes in precipitation, temperature, climate and adult female density. Parturition date was mostly driven by autumn weather, suggesting that reproductive phenology in large mammals may be more dependent on variation in the timing of ovulation rather than in spring or summer resource acquisition.

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## Compliance with ethical standards

**Ethical standards** Animals were captured and handled in compliance with the Canadian Council on Animal Care, under the approval of the Université de Sherbrooke Animal Care Committee (protocol number FP-2016-01 and MFB-2014-01—Université de Sherbrooke).

**Conflict of interest** The authors declare that they have no conflict of interest.

**Data availability** The datasets analysed during the current study are available from the corresponding author on reasonable request.

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