

Onset of autumn shapes the timing of birth in Pyrenean chamois more than onset of spring

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Summary

1. In seasonal environments, birth dates are a central component for a species' life history, with potential long-term fitness consequences. Yet our understanding of selective pressures of environmental changes on birth dates is limited in wild mammals due to the difficulty of data collection. In a context of rapid climate change, the question of a possible mismatch between plant phenology and birth phenology also remains unanswered for most species.

2. We assessed whether and how the timing of birth in a mountain mammal (isard, also named Pyrenean chamois, *Rupicapra pyrenaica pyrenaica*) tracked changes in plant growing season, accounting for maternal traits, individual heterogeneity and population density. We not only focused on spring conditions but also assessed to what extent onset of autumn can be a driver of phenological biological events and compared the magnitude of the response to the magnitude of the environmental changes. We relied on a 22-year study based on intensively monitored marked individuals of known age.

3. Births were highly synchronized (80% of kids born within 25 days) and highly repeatable (84%; between-female variation of 9.6 days, within-female variation of 4.2 days). Individual phenotypic plasticity allows females to respond rapidly to interannual changes in plant phenology but did not prevent the existence of a mismatch: a 10-day advance in the autumn or spring plant phenology led to 3.9 and 1.3 days advance in birth dates, respectively.

4. Our findings suggest that plant phenology may act as a cue to induce important stages of the reproductive cycle (e.g. conception and gestation length), subsequently affecting parturition dates, and stressed the importance of focusing on long-term changes during spring for which females may show much lower adaptive potential than during autumn. These results also question the extent to which individual plasticity along with high heterogeneity among individuals will allow species to cope with demographic consequences of climate changes.

Key-words: birth phenology, isard, marked animals, onsets of spring and autumn, Pyrenean chamois, repeatability, *Rupicapra pyrenaica pyrenaica*

Introduction

In large herbivores, timing and synchrony of births with availability of resources have important consequences on population dynamics through their effects on off-spring mass (Albon, Clutton-Brock & Guinness 1987; Solberg *et al.* 2007; Feder *et al.* 2008) and growth rate (Albon, Clutton-Brock & Guinness 1987; Clutton-Brock *et al.* 1992; Andersen & Linnell 1997), which in turn influence juvenile survival (Bunnell 1980; Albon, Clutton-Brock & Guinness 1987; Clutton-Brock *et al.* 1987;

Festa-Bianchet 1988; Birgersson & Ekvall 1997; Feder *et al.* 2008), and have the potential to generate cohort effects (Gaillard *et al.* 2003) with long-lasting fitness consequences (Albon, Clutton-Brock & Guinness 1987; Gaillard *et al.* 1996; Solberg, *et al.* 2004, 2007). Thus, understanding factors influencing birth dates and synchrony has strong evolutionary and management implications for these species (Keech *et al.* 2000; Feder *et al.* 2008).

Among these factors, climate plays an important role in shaping birth patterns of most ungulates living in seasonal environments. Births typically are timed so that the high energetic demands of late gestation and early lactation (Rutberg 1987; Clutton-Brock, Albon & Guinness 1989)

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coincide with the greatest seasonal forage availability and quality (early stages of plant phenology), as well as relatively benign weather (Bunnell 1980; Rutberg 1987; Bowyer 1991; Rachlow & Bowyer 1991) which corresponds to early spring in temperate areas. To match births to this period, ungulates can either adjust their conception date (Langvatn *et al.* 2004; Garel *et al.* 2009) and/or their gestation length (Berger 1992; Ryan, Knechtel & Getz 2007; Scott *et al.* 2008; Clements *et al.* 2011). Environmental variables such as food availability and temperatures may act as cues to induce these important stages of their reproductive cycle. For instance, in domestic animals, ambient temperatures impact the onset of the breeding season (Dutt & Bush 1955; Godley, Wilson & Hurst 1966; Sadleir 1969; Fisher & Johnstone 2002). Therefore, lower temperatures and plant senescence appearing at the onset of autumn are likely to initiate conception in wild herbivores and could thus be a driver of phenological biological events in species living in seasonal environment, although it has to our knowledge rarely been investigated in temperate species. Likewise, milder temperatures and vegetation flush occurring at the onset of spring might warn females to shorten their gestation length and induce earlier parturition. Accordingly, it has been shown that change in the timing of peak resource availability generated a change in timing of breeding dates in birds (e.g. Dunn & Winkler 1999; Charmantier *et al.* 2008; Reed *et al.* 2009), but similar studies still remain rare in large mammals (Moyes *et al.* 2011). Understanding the changes in birth dates under different environmental conditions at an individual level contributes to understanding the role of phenotypic plasticity in population responses to climate change (McNamara & Houston 1996; Nussey, Wilson & Brommer 2007; Charmantier *et al.* 2008). Further, the role that phenotypic plasticity plays is important for understanding the current and likely future fitness consequences of climate change as recently highlighted in roe deer, where the absence of phenotypic plasticity in birth dates has led to a mismatch between environmental changes and birth phenology, slowing down the population demography of this species (Plard *et al.* 2014).

While it can be beneficial for all females to adjust the timing of birth to variable environmental conditions, parturition dates also vary among mothers, especially according to the physiological state of females (McNamara & Houston 1996) which depends on individual characteristics such as age or previous reproductive attempts (Festa-Bianchet, Gaillard & Jorgenson 1998; Hamel *et al.* 2010). For instance, prime-age females come into oestrus earlier (Langvatn *et al.* 2004; Garel *et al.* 2009) and consequently give birth before younger or older ones (Clutton-Brock *et al.* 1992; Adams & Dale 1998; Cook *et al.* 2004; Feder *et al.* 2008). Similarly, females that have raised their offspring to weaning tend to come into oestrus later, and therefore have delayed parturition dates (Guinness, Clutton-Brock & Albon 1978; Adams & Dale 1998; Testa & Adams 1998; Feder *et al.* 2008) due to reproductive costs.

Late conception dates have also been documented for several species as a result of increasing population densities: due to fewer resources per capita, females enter the rut in poorer condition (Clutton-Brock *et al.* 1987; Festa-Bianchet 1988; Langvatn *et al.* 2004; see Bonenfant *et al.* 2009 for a review). Life history strategies can also differ within individuals during their lifetimes, showing individual plasticity in response to changing environmental conditions (van de Pol & Verhulst 2006; Nussey *et al.* 2008; Senapathi *et al.* 2011; Balbontín *et al.* 2012). Complex interacting processes (due to female's own quality, female's reproductive history, current or past environmental conditions, population structure) can therefore generate changes in the timing of birth, exemplifying that phenological consequences of climatic changes should be studied together with detailed longitudinal information on individual and population characteristics (Coulson, Milner-Gulland & Clutton-Brock 2000; Forchhammer *et al.* 2001).

Here, we studied a population of isard (*Rupicapra pyrenaica pyrenaica*, also named Pyrenean chamois) intensively monitored over a 22-year period by capture-mark-recapture. This population offers a rare opportunity to assess whether and how the timing of births in female isard tracked environmental changes, while accounting for individual and population characteristics expected to cause variation in the parturition date (Table 1). In addition, longitudinal data allowed us to estimate within-individual heterogeneity relative to between-female differences (i.e. individual repeatability ShROUT & Fleiss 1979) and to assess to what extent individual plasticity may have occurred in response to environmental changes (Nussey, Wilson & Brommer 2007; Charmantier *et al.* 2008). We compared the magnitude (in number of days) of the response to the magnitude of the environmental changes and focused on the effects of both spring and autumn conditions, following recent studies (e.g. Hurley *et al.* 2014) that demonstrated that autumn conditions, though often ignored in temperate ecosystems, could be decisive for animal condition. Specifically, we hypothesized that early onset of autumn in year $t-1$ and early onset of spring in year t would lead to early births in year t because of their effects on access to vegetation and on environmental conditions.

Materials and methods

STUDY AREA AND POPULATION

We studied the isard population of Bazès in the foothills of the French Western Pyrenees (43.00°N, 0.23°W; 1000–1800 m a.s.l.), from 1986 to 2011. The study area covers approximately 400 ha, dominated mostly by forest (beech *Fagus sylvatica* and firs *Abies* sp.) and alpine grass (*Festuca eskia*). During the study period, the average (\pm SD) annual minimum and maximum daily temperatures were $5.2 \pm 5.4^\circ\text{C}$ and $14.4 \pm 7.2^\circ\text{C}$, respectively. Total annual precipitations reached 1151.1 ± 150.4 mm. Isard have no natural predators in the study area, except for red foxes (*Vulpes vulpes*) that may occasionally predate on newborns and sick isard.

Table 1. Description and predictions of the effects of each variable tested on the timing of birth in the Bazès, France isard population (1986–2011)

Sources of variation in birth dates	Expected effect	Associated variables	Description
Demographic periods	Females give birth earlier during the colonizing period than during the stabilizing period	demo	2 levels (1986–2001 and 2002–2011)
	The later births were observed the year of the population crash. In the other years, females gave birth earlier during the colonizing period than during the stabilizing period	democrash	3 levels (1986–2001, 2002, 2003–2011)
	Same as previous effect but with a lagged effect of the population crash in the subsequent year	democrashlag	4 levels (1986–2001, 2002, 2003, 2004–2011)
	No effect of colonizing/stabilizing. Delay in births after the population crash	crash	2 levels (2002 and ‘other years’)
	Same as previous effect with a lagged effect in the subsequent year	crashlag	3 levels (2002, 2003 and ‘other years’)
Age	Young females (most being primiparous) give birth later than adult females (most being multiparous)	age2cl	2 levels (2- to 3-years-old and ≥ 4 -years-old)
	Young females give birth later than adult females and among adult females, old females give birth (<i>i</i>) later than prime age females because of their poorer conditions or (<i>ii</i>) earlier in accordance with the terminal investment theory	age3cl	3 levels (2- to 3-years-old, 4- to 11-years-old and ≥ 12 -years-old)
Reproductive status	Females with no young during the rut reproduce earlier than reproductive females with young as they had no reproductive cost the previous year, and females that lost young reproduce earlier than females with young all year around	rs	3 levels (‘no young’, ‘lost young’ and ‘with young’)
Plant phenology	Earlier births the year following early onset of autumn	oa	Continuous variable ranging from September 28 to November 21
	Earlier births the year with early onset of spring	os	Continuous variable ranging from March 11 to May 20

Mating occurs from mid-November to early January with males engaging primarily in tending and blocking behaviour to maintain exclusive access to oestrous females (*sensu* Clutton-Brock 1989; Loison 1995). Gestation period lasts for 160–170 days, and females give birth to one kid in spring (see Results section). Females are able to reproduce for the first time at the age of 2, and the maximum known longevity reached for a female has been 21 years in our population.

The population originated from part of the release of 34 individuals in 1984–1985 from the Pyrenean National Park (Loison *et al.* 2006), after its local disappearance in the 1950s. All founders were marked with coloured collars. From 1990 to 2010, females were captured mainly using leg-hold snares during spring and autumn. Every individual was aged using horn-ring counts (Schröder & Von Elsner-Schak 1985). The reproductive status of marked females was determined by observing the presence/absence of a young at heel, during intensive field monitoring from spring to autumn. In this population, first breeding occurred at the age of 2 or 3 years depending on the demographic periods (see below), so that most females ≥ 4 -years-old can be reasonably considered as multiparous.

Over the study period, the population experienced two contrasted demographic periods. A colonizing period with a strong population increase rate ($r = 0.25$), from the introduction to 2001, when the population size peaked at *ca.* 200 individuals (Loison *et al.* 2002), and a period of stabilization after 2002, when the population size fluctuated between 100 and 130 individuals (Fig. 1). The periods are delimited by an accidental intoxication that occurred in late May–July 2001 and caused the death of >60 individuals. We tested five different period effects, accounting for the difference between the 2 demographic periods (colonizing/

stabilizing) and/or for the effect of population crash (on 2002 births only) with, or without, a potential lagged effect (on 2002 and on 2003 births; Table 1).

ENVIRONMENTAL CONDITIONS

We used two indices of vegetation growing season (onset of spring and onset of autumn; Table 1) computed from daily mean (*tmean*) and daily minimum (*tmin*) temperatures. We chose to define the onset of spring as being the last day of the first 6-day period, after the last winter/spring frost, in which daily means were $\geq 5^\circ\text{C}$ (Walther & Linderholm 2006). We defined the last day of frost as the last day when *tmin* $< 0^\circ\text{C}$ (Menzel *et al.* 2003). We computed the onset of autumn as the first day of the first 10-day period with a mean temperature of $< 5^\circ\text{C}$ (Linderholm, Walther & Chen 2008). We used a threshold of *tmean* = 5°C for determining the thermal growing season (Menzel *et al.* 2003; Linderholm 2006; Linderholm, Walther & Chen 2008; Moyes *et al.* 2011).

Meteorological data were recorded at the Meteo France weather station in Arrens-Marsous (42.95°N, 0.22°W, 910 m a.s.l.), about 5 km from the Bazès site.

STATISTICAL ANALYSIS

Computing birth dates

For a given female and a given year, birth data were estimated from the last day the same female was seen without her young (t_1) and the first day she was seen with it (t_2). Extreme outliers of t_2 were extracted from the data set ($< 1\%$ of the data), and we subse-

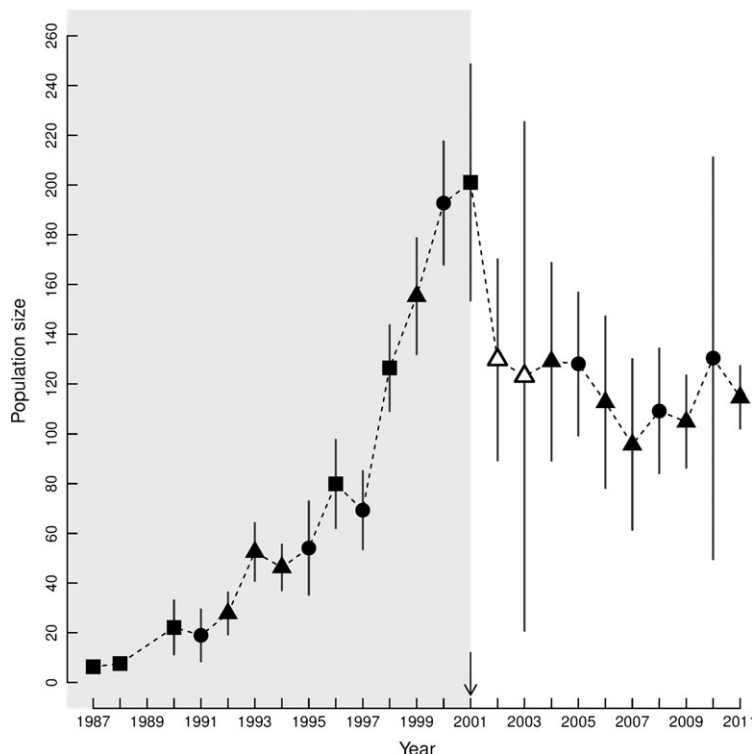


Fig. 1. Population size estimates of isard using capture-mark-resighting (CMR) from 1987 to 2011 in Bazès, France (Arnason, Schwarz & Gerrard 1991). Estimates are the mean value between the previous year summer and autumn and the current year spring capture-mark-recapture estimates, weighted by the standard error obtained for each estimate (Loison *et al.* 2006). Squares, dots and triangles represent years where, respectively, only one, two or three seasons are available. The area coloured in grey indicates the colonizing period and the white area the stabilizing period. Uncoloured dots show years possibly affected by the catastrophic event which occurred in 2001 (arrow).

quently computed birth dates only when $t_2 - t_1 < 32$ days (80.4% of the data). Birth dates can be computed as the median date within this interval $t_2 - t_1$ (e.g. Côté & Festa-Bianchet 2001). However, birth dates are expected to be normally (Gaillard *et al.* 1993; Keech *et al.* 2000) or log-normally distributed (Festa-Bianchet 1988; Sigouin, Ouellet & Courtois 1997; Bowyer, Van Ballenberghe & Kie 1998; Rubin, Boyce & Bleich 2000), that is not uniformly. In such conditions, birth dates are more likely to be asymmetrically distributed within the interval $t_2 - t_1$ when births occur close to the tails of the distribution. We thus performed a two-step procedure to account for biological distribution of birth dates and get the most reliable estimates within this interval (see Supporting Information Appendix S1 for more details). First, we fitted normal and log-normal distributions to a subset of the data for which $t_2 - t_1 < 5$ days and selected the best adjusted distribution. We considered the median date within this very short interval as the exact date of birth (see e.g. Côté & Festa-Bianchet 2001). We assessed the goodness of fit of the best distribution by a Pearson χ^2 test (Agresti 2002) and calculated the parameter estimates of this distribution (μ , mean birth date and σ^2 , a measure of birth synchrony). Second, we estimated birth dates from all the data (i.e. where $t_2 - t_1 < 5$ days and $5 \text{ days} < t_2 - t_1 < 32$ days) as the quantile function of the mean between the distribution function of t_1 and t_2 knowing μ and σ . We also computed the number of consecutive days during which 80% of births took place over each year as a measure of birth synchrony (e.g. Rutberg 1987; Bowyer 1991; Côté & Festa-Bianchet 2001).

Assessing biological hypotheses

We used linear mixed models with females' identity as a random effect on the intercept to account for within-individual dependency (Pinheiro & Bates 2000; van de Pol & Verhulst 2006). Testing for variation between females in their plastic response to phenological changes could be done by including ran-

dom effects on environmental covariates (i.e. on slopes; e.g. Nussey *et al.* 2005b; Charmantier *et al.* 2008). However, the fit of such models led to a convergence problem as indicated by a correlation of 1 between random effects (that cannot be fixed by centring predictors as commonly advised), suggesting that the model may be overparametrized. Each birth date was weighted by $1/d$ with $d = t_2 - t_1$, in order to give more weight to birth dates obtained with a small length of time between t_1 and t_2 .

When assessing the effect of environmental changes on timing of birth (variables related to 'plant phenology' in Table 1), we also accounted for individual and population characteristics expected to cause variation in the parturition date. First, we expected that births would occur earlier in more favourable conditions (Clutton-Brock *et al.* 1987; Festa-Bianchet 1988; Langvatn *et al.* 2004) that is, when the population was in a colonizing process (Loison *et al.* 2002; variables related to 'demographic periods' in Table 1). We also quantified the effect on birth dates of a catastrophic event the population experienced (namely an accidental intoxication during which *ca.* 40% of the females died) and hypothesized a delay of births in the subsequent years. Second, we predicted that young females would give birth later than prime-aged females (Clutton-Brock *et al.* 1992; Adams & Dale 1998; Cook *et al.* 2004; Feder *et al.* 2008) and that old females would either delay birth due to their poorer body condition (Gaillard *et al.* 2000) or give birth earlier to maximize their offsprings' chance of survival in accordance with the terminal investment theory (Clutton-Brock 1984; variables related to 'Age' effects in Table 1). Assuming a cost of reproduction (Festa-Bianchet, Gaillard & Jorgenson 1998; Hamel *et al.* 2010), we expected females with no young to wean to give birth earlier than other females in the subsequent year (variables related to 'reproductive status' in Table 1).

We assessed whether a given female gave birth at approximately the same date each year (repeatability of birth dates) by computing the ratio between the variance in the random effect (the mother's identity) and the total variance of the model (the

intraclass correlation coefficient *sensu* Shrout & Fleiss 1979; McGraw & Wong 1996), using values from the selected model.

Finally, from a subset of females that bred in consecutive years, we computed the within-female change in birth dates (birth date_{*t*} – birth date_{*t-1*}) between pairs of years and the corresponding interannual changes in phenological variables selected in the best model. We then used a mixed model with the female's identity as a random intercept, weighted by average 1/*d* between the consecutive birth dates, to estimate the slope of the relationship between these two quantities. Slopes of this regression provide a direct estimate of individual plastic responses to phenological changes that can be compared to the slope of the global model on birth dates including the corresponding variables (see Charmantier *et al.* 2008 for a similar approach). Similar slopes indicate that most of the females' responses to phenological changes can be explained by individual plasticity in behaviour.

Model selection

For estimations of birth dates, model selection was performed using Akaike information criterion with second-order adjustment, AIC_c, to correct for small sample bias (Burnham & Anderson 2002). When the difference in AIC_c (ΔAIC_c) is greater than 2, there is considerable support for a real difference between models (Burnham & Anderson 2002). In the footsteps of Zuur *et al.* (2009), we performed model selection of mixed models based on the maximum likelihood method (ML), and the final model was fitted using REML to get parameter estimates. For the selected model, we also checked for the absence of any residual structure, which corroborated our choice. Restricting the data set to females breeding twice or more qualitatively yielded similar results. All analyses were performed using R version 3.0.2 (R Development Core Team 2011) and lme4 packages for mixed models (Bates *et al.* 2013) and MuMIn for multimodel inference approach (Bartón 2013).

Results

DATA SET AND PARAMETER ESTIMATION OF BIRTH DATES DISTRIBUTION

We had 28 birth dates for which $t_2 - t_1 < 5$. The distribution of parturition dates was slightly better described

by a normal distribution (AIC_c = 242.16) than a log-normal distribution (AIC_c = 242.21; ΔAIC_c = 0.05). The normal distribution fitted our data well (Pearson chi-squared test, $\chi^2 = 2.43$, d.f. = 3, $P = 0.49$) with the mean date of birth being $\mu = 143.8$ (24th of May) and the standard deviation $\sigma = 16.9$ days (Fig. S1).

With 237 estimated birth dates from 74 females across 22 years (1986–2011, no data in 1987, 1989, 1991 and 1995), we recorded 3.2 ± 2.3 births per female. Using only years with more than 10 birth dates ($n = 11$ years, mean = 17.2 dates per year, from 11 to 25 dates), we found that 80% of births took place in 25.1 days with a coefficient of variation of 38.9%.

ASSESSING BIOLOGICAL HYPOTHESES, REPEATABILITY AMONG FEMALES AND PHENOTYPIC PLASTICITY

Our best model included the effects of population crash (partial $R^2 = 0.04$), of age (young vs. adult females; partial $R^2 = 0.05$), of reproductive status (partial $R^2 = 0.15$) and of both phenological variables (onset of autumn, partial $R^2 = 0.13$; onset of spring, partial $R^2 = 0.04$; Table 2). Colonizing and stabilizing periods of density had no effect on birth date. This model accounted for a large amount of variation in birth dates ($R^2 = 0.40$). We also found a marked repeatability of birth dates (83.9%) with a within-female standard deviation of 4.2 days and a between-female standard deviation of 9.6 days.

In the following results, we reported effect sizes for the factor levels 'other years' (variable 'crash'), 'with young' (variable 'rs'), '≥4-years-old' (variable 'age2cl') and for the average date of onset of spring (111.13 days) and autumn (296.04 days; Table 3). The average date of birth was delayed by 15.3 days in 2002 (2 June [22 May; 13 June]_{95%}) compared with other years (18 May [14 May; 21 May]_{95%}). Taking into account the lag effect ('crashlag'; Table 2) did not improve the model (ΔAIC_c = 2.04). Similarly, considering the two demographic periods alone ('demo'), with the crash effect ('democrash') or with the

Table 2. Model selection with the demographic periods effect, age class, the previous year reproductive status, onset of autumn and spring on the timing of births in the Bazès, France isard population, 1986–2011 (see Table 1 for hypotheses tested). Each model contains females' identity as a random effect on the intercept. DF indicates the number of estimated parameters. For factors, (×) means that the variable is selected in the model; for continuous covariates, the slope is reported when the variable is selected. We only present models with a ΔAIC_c < 4, models including only one variable at a time among the variables selected in the best model and the null model

Intercept	Period	Age	Onset of autumn	Onset of spring	Reproductive status	d.f.	ΔAIC _c
2.72	crash	agecl2	0.39	0.13	×	9	0.00
1.42	crashlag	agecl2	0.39	0.13	×	10	2.04
13.50	crash	agecl3	0.39	0.13	×	10	2.14
2.43	democrash	agecl2	0.39	0.13	×	10	2.16
135.62	–	–	0.41	–	–	4	29.12
138.48	–	–	–	–	×	4	40.91
134.83	–	agecl2	–	–	–	4	51.21
135.20	crash	–	–	–	–	4	51.38
122.38	–	–	–	0.12	–	4	52.45
135.62	–	–	–	–	–	3	55.94

lag effect ('democrashlag'), did not improve the model fit ($\Delta AIC_c > 2.16$; Table 2).

Young females (most being primiparous) have delayed parturition dates of 12.5 days (30 May [20 May; 9 June]_{95%}) compared with ≥ 4 -years-old females (18 May [14 May; 21 May]_{95%}). Model including age class as a factor with 3 levels ('age3cl', Table 1) had a lower support ($\Delta AIC_c = 2.14$).

Females with no young to wean gave birth 5.3 days (12 May [6 May; 19 May]_{95%}) earlier than females whose young survived to 1 year (18 May [14 May; 21 May]_{95%}). Females that had a young the previous year that died before reaching 1 year gave birth the earliest (9 May [5 May; 14 May]_{95%}) with 8.2 days difference with successful mothers.

When the onset of autumn the previous year was delayed by 10 days, parturition dates were postponed by 3.9 days the following spring (estimated slope of

0.39 days [0.248; 0.528]_{95%}, Fig. 2). Similarly, a delay of 10 days of the onset of spring retarded parturition by 1.3 days during spring (estimated slope of 0.133 days [0.039; 0.227]_{95%}, Fig. 3).

Finally, the slopes of the relationship between within-female changes in birth dates (from females that bred in consecutive years) and interannual changes in onset of autumn (slope, SE: 0.329, 0.113) and spring (0.113, 0.058) were closely similar to the one obtained from the best model on birth dates (Table 3).

Discussion

Studies linking environmental changes to changes in phenological events through phenotypic plasticity are still scarce in large mammals (e.g. Plard *et al.* 2014), especially in mountain environments where data gathering has always been hindered by logistical constraints in the field. Moreover, studies of birth phenology have mostly focused so far on the effect of spring plant phenology, ignoring the possible role of autumn phenological characteristics. Our study contributes by going a step further and by providing some of the first evidence in mountain ungulates that females are able to respond to phenological changes by adjusting their parturition dates, giving birth later with delayed onset of autumn and spring. Interestingly, we quantified the magnitude of this response and showed that the onset of autumn had a much stronger effect than the onset of spring and that animals only partly track the magnitude of environmental changes. We also found that the date at which a female gives birth was highly repeatable over a number of years, with repeatability values

Table 3. Parameter estimates and standard errors for the selected model (see Table 2), for the factor levels 'other years' (variable 'crash'), ≥ 4 -years-old (variable 'agecl2') and 'with young' (variable 'rs').

Parameter	Estimate	SE	<i>t</i>
Intercept	8.02	23.15	0.35
Period effect in 2002	15.26	5.45	2.80
2- to 3-years-old females	12.45	4.62	2.70
Females no young	-5.30	3.38	-1.57
Females lost young	-8.19	2.20	-3.72
oa	0.39	0.07	5.43
os	0.13	0.05	2.76

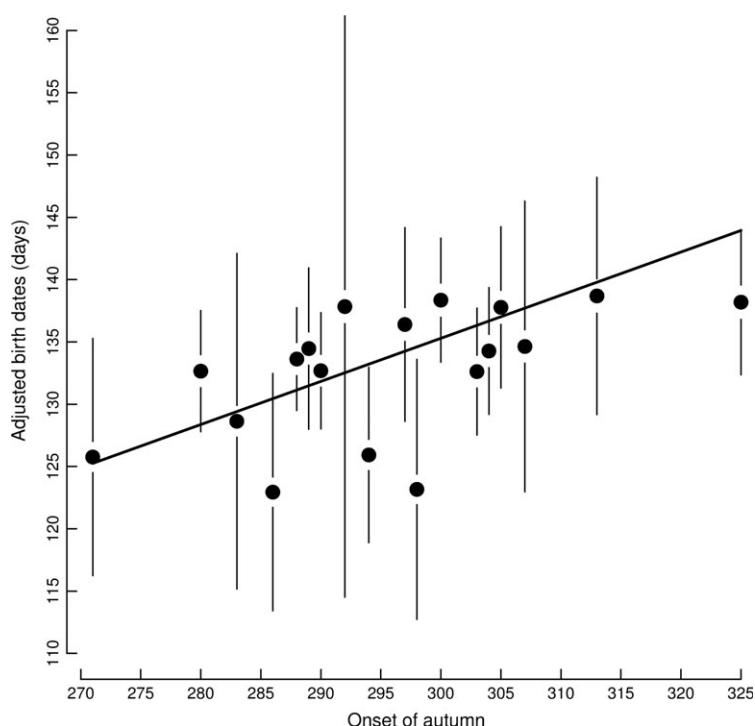
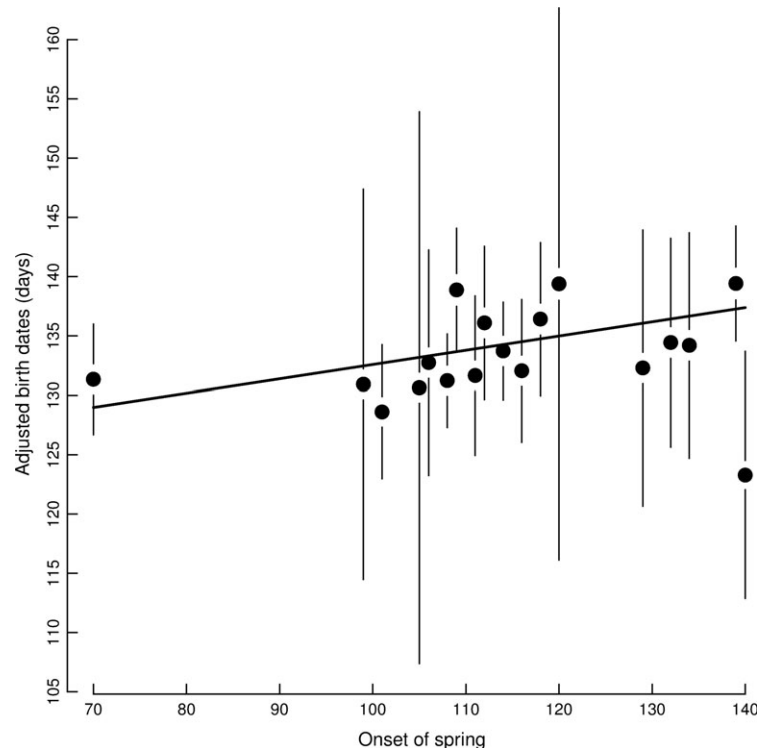


Fig. 2. Relationships between onset of autumn and birth dates of isard monitored at Bazès (France) between 1986 and 2011. Filled circles are the mean values (for each onset of autumn value; with some years having the same oa values) of a linear model adjusted for the effects of variables crash, reproductive success, age and onset of spring (see Table 1 for variable description and Table 2 for model selection). The solid line represents the predicted values of the linear model. Day 300 corresponds to October 27th.

Fig. 3. Relationships between onset of spring and birth dates of females isard monitored at Bazès (France) between 1986 and 2011. Filled circles are the mean values (for each onset of spring value; with some years having the same onset values) of a linear model adjusted for the effects of variables crash, reproductive success, age and onset of autumn (see Table 1 for variable description and Table 2 for model selection). The solid line represents the predicted values of the linear model. Day 110 corresponds to April 20th.



among the highest reported in large mammals (see also Plard *et al.* 2013 in roe deer), but did not jeopardize the existence of phenotypic plasticity.

As expected for an ungulate living in a temperate environment, birth dates were synchronous at the population level (e.g. Bowyer 1991; Gaillard *et al.* 1993; Côté & Festa-Bianchet 2001; Meng *et al.* 2003) with 80% of births occurring in 25.1 days around the month of May, corresponding to the period when the vegetation has flushed and resources are abundant. Similarly, in accordance with previous studies (e.g. Clutton-Brock *et al.* 1992; Testa & Adams 1998; Feder *et al.* 2008), births were delayed for younger females and for those suffering from previous costs of reproduction. We found that females that gave birth and lost their kid tend to give birth earlier than females that did not give birth. This finding might be explained by heterogeneity in individual quality: females that reproduce would be of 'better quality' than those that do not, and therefore reach reproductive condition earlier than the non-reproductive females when not bearing rearing cost (Weladji *et al.* 2008). We also found a 2-week delay in births the year following the catastrophic event that our population experienced.

Later onset of autumn delayed parturition the following spring, most likely because low temperatures and therefore decreased vegetation quality may act as a cue to induce conception. Indeed, ambient temperature has been recorded to affect the timing of the onset of breeding season in domestic animals (Dutt & Bush 1955; Godley, Wilson & Hurst 1966; Sadleir 1969; Fisher & Johnstone 2002). In pasture-farmed red deer hinds, an earlier calving date of 3 days for every 1°C drop in minimum air temper-

ature during the rut was reported (Fisher & Johnstone 2002). This might come from an advanced oestrus when in presence of low temperatures. Hampshire-crossed Western ewes placed in experimental air-conditioned rooms came into oestrus almost eight weeks before the control females, with exactly the same food supply (Dutt & Bush 1955).

In addition to what was found for domestic animals, the onset of autumn could also have an effect on the birth dates by driving the timing of males' rutting activities. In ungulates, males in rut shift to an energy-saving strategy in which they cease feeding activities (Myserud *et al.* 2008). They have to gain the maximum amount of energy before the rutting period, and may therefore continue feeding as long as possible (late onset of autumn) before they allocate this energy to reproduction. In fact, younger red deer males, who cannot compete with older males, enter reproduction later (Miquelle 1990) and therefore privilege eating longer and putting resources into body growth before reproduction (Myserud *et al.* 2008). The same pattern might arise for male isard when the growing season lasts longer: they tend to take advantage of feeding before entering costly rutting activities. The delay of the rutting period induced by the longer availability of food linked to a late autumn could explain why births occur later the following spring.

Early onset of spring was related to earlier parturition dates the same year. This result highlights the fact that there might be some plasticity in gestation length in isard in response to environmental conditions. In fact, gestation length adjustment has been discussed as a reproductive tactic of large mammals in seasonal environments (Berger

1992; Mysterud *et al.* 2009; Clements *et al.* 2011). Late-breeding bison females in good condition were able to shorten gestation length to up to 15 days, to synchronize their births with other females (Berger 1992). As the onset of spring is measured through temperature, our findings follow those of Clements *et al.* (2011), which found shorter gestation lengths in red deer when March temperatures were high. These high spring temperatures might explain increased nutritional availability provoked by increased grass growth and may simply enable faster foetal growth rate (Clements *et al.* 2011). Indeed, increased nutrition during the last trimester of pregnancy decreased gestation length in captive red deer (Asher *et al.* 2005). Simultaneously, females may influence growth rates of their foetuses as a tactic to give birth within an optimum window, with spring temperatures acting as a cue that the optimum birth time is likely to be earlier (Clements *et al.* 2011).

Our findings suggested that most of the females' responses to changes in onset of autumn and spring can be explained by individual plasticity in birth date as slopes obtained from the regression of within-individual changes between consecutive years and interannual changes in environmental conditions led to the same estimates as our global approach (Charmantier *et al.* 2008). Another line of evidence showed more support for phenotypic plasticity than for micro-evolutionary response to natural selection caused by climate changes. Indeed, our environmental conditions varied considerably from year to year (Fig. S2) without any linear trend over the study period. In such a context, micro-evolution might not lead to year-to-year changes in phenotype that could explain the relationship reported here (e.g. Fig. 2), especially in a species for which the generation time is >5 years (Crampe *et al.* 2006).

This finding has implications for understanding the future fitness consequences of climate changes for Pyrenean chamois and opens discussions on the role of phenotypic plasticity in this context. Whereas the plasticity in individual response that allows individuals to track changes in environmental conditions has been reported in red deer (Moyes *et al.* 2011), Pyrenean chamois (this study) and several bird species (Dunn & Winkler 1999; Charmantier *et al.* 2008; Reed *et al.* 2009), investigation of how the magnitude of this response follows the magnitude of the environmental changes has so far often been neglected. Here, by translating changes in climatic conditions in terms of onset of phenological events, we were able to measure this potential mismatch and showed that a 10-day advance in the autumn or spring plant phenology led to a 3.9 and 1.3 days advance in birth dates, respectively. This result leads us to question whether individual plasticity (within-female standard deviation of 4.2 days) along with heterogeneity among individuals (between-female standard deviation of 9.6 days), which shed light on the potential for micro-evolution, would be enough to allow this population to cope with demographic consequences of climate changes over the long term. A recent

study in roe deer reported mismatch between birth phenology and environmental changes, with subsequent important consequences on population demography (Plard *et al.* 2014). Like for roe deer (54–93%; Plard *et al.* 2013), we found a high individual repeatability in birth dates in Pyrenean chamois (84%). This measure is exceptionally high when compared to red deer, for which the repeatability of birth dates is only 10% (Nussey *et al.* 2005a). As Plard *et al.* (2013) suggested, this high repeatability measure could indicate low plasticity in this life history trait, showing that individuals have little potential to respond rapidly to drastic changes. However, this high repeatability in our population originated from large interindividual variation as compared to intra-individual variation (see values above and Results). Unlike roe deer, isard were thus able to partly track rapid changes in environmental conditions, while also offering potential for micro-evolution, both of which might allow them to better perform when faced with climate changes over the long term. This difference exemplifies that high repeatability does not necessarily involve low phenotypic plasticity.

Finally, our findings showed that the effect of the onset of autumn on birth timing is markedly more important than the effect of the onset of spring or, alternatively, that females were more constrained in adjusting the timing of births in response to spring conditions than to autumn conditions. This result probably had a mechanical explanation with females being less constrained in adjusting the timing of oestrus than gestation length. It also stressed the need for future research to focus on the demographic consequence of environmental changes occurring in spring, a period which increasingly appears as the critical period for species living in mountain area (Pettorelli *et al.* 2007; Garel *et al.* 2011).

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Data accessibility

Data used within this manuscript are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pf420> (Kourkgy *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Computing birth dates.

Figure S1. Distribution of observed birth dates for which $t_2 - t_1 < 5$ days (Julian date; $n = 28$; white histogram) and theoretical distribution (grey histogram) following a normal distribution ($\mu = 143.8$ days and $\sigma = 16.9$ days). Day 144 corresponds to May 24th.

Figure S2. Yearly variation in average birth dates (weighted mean \pm SD; see Methods for details on weights computation), onset of autumn and onset of spring in the Bazès, France isard population, 1986–2011. Day 144 corresponds to May 24th.