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Never too late? Consequences of late birthdate for mass and survival of bighorn lambs

Chiarastella Feder · Julien G. A. Martin · Marco Festa-Bianchet · Céline Bérubé · Jon Jorgenson

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Abstract In strongly seasonal environments, the timing of birth can have important fitness consequences. We investigated which factors affect parturition date and how birthdate interacts with sex, maternal characteristics and environmental variables to affect the growth and survival of bighorn sheep (*Ovis canadensis*) lambs in a marked population in Alberta. Over 14 years, the estimated birthdate of 216 lambs ranged from 21 May to 18 July. Parturition date was heritable and genetically correlated with maternal mass the previous fall. Weaning a lamb delayed parturition the following year by about 7 days. Birthdate did not affect summer growth rate, but late-born lambs were lighter in mid September (the approximate time of weaning) than early-born ones. Birthdate did not affect survival to weaning, but late birth decreased survival to 1 year for male lambs. Forage quality, measured by fecal crude protein, did not affect survival to 1 year. Once we accounted for lamb mass in mid September, birthdate no longer affected the probability of survival, suggesting that late birth decreased survival by shortening a lamb's growing season. Because there was no compensatory summer growth, late-born lambs were smaller than early-born ones at the onset of winter. Our data highlight the importance of birthdate on life history traits and suggest that resource scarcity had more severe consequences for juvenile males than for females.

Keywords Dimorphic species · Sex · Heritability · Parturition date

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C. Feder · J. G. A. Martin · M. Festa-Bianchet · C. Bérubé
Département de Biologie, Université de Sherbrooke,
Sherbrooke, QC J1K 2R1, Canada
e-mail: julien.martin2@usherbrooke.ca

J. G. A. Martin · M. Festa-Bianchet (✉)
Centre d'Études Nordiques, Université Laval,
Pavillon Abitibi-Price, local 1202, Quebec,
QC G1K 7P4, Canada
e-mail: marco.festa-bianchet@usherbrooke.ca

J. Jorgenson
Fish and Wildlife Division,
Department of Sustainable Development,
Box 1059, Canmore, AB T0L 0M0, Canada

Introduction

Early development can have important fitness consequences by affecting survival, fecundity or age of first reproduction (Lindström 1999). For large herbivores in highly seasonal habitats with short growing seasons, the timing of birth is closely synchronized with vegetation phenology, and late birth can lower juvenile survival (Côté and Festa-Bianchet 2001; Fairbanks 1993; Festa-Bianchet 1988a; Green 1993). It is therefore important to identify both the factors that affect birthdate and the effects of birthdate on juvenile growth and survival, which may also affect population dynamics.

For most temperate and northern ungulates, reproduction is highly seasonal (Berger 1992; Côté and Festa-Bianchet 2001; Festa-Bianchet 1988a). Typically, 80% or more of births occur within 2 weeks of the first parturition, with a few births occasionally recorded up to 2 months later [Festa-Bianchet 1988a, for bighorn sheep; Fairbanks 1993, for pronghorn (*Antilocapra americana*); Côté and Festa-Bianchet 2001, for mountain goats (*Oreamnos americanus*)]. Individuals born late may be unable to accumulate sufficient reserves to survive the winter (Côté and

Festa-Bianchet 2001; Festa-Bianchet 1988a). For example, in a bighorn sheep population where most births occurred between 20 May and 5 June, only 5% of lambs born after 10 June survived to 1 year of age, compared to 44% survival for lambs born earlier (Festa-Bianchet 1988a).

Birthdate has important consequences for traits such as birth and weaning mass, summer growth rate and survival (Côté and Festa-Bianchet 2001; Fairbanks 1993; Festa-Bianchet 1988a; Green and Rothstein 1993). Although several studies have shown a survival advantage for early-born juveniles (Clutton-Brock et al. 1983; Côté and Festa-Bianchet 2001; Festa-Bianchet 1988a), little is known about the factors that affect individual variation in parturition date in wild ungulates, or the mechanisms that reduce survival of late-born juveniles. Individual quality (Kruuk et al. 1999), previous reproductive success (Clutton-Brock et al. 1984), previous breeding experience (Green and Rothstein 1991) and age (Festa-Bianchet 1988b) could explain some of the variability in birthdate (Clutton-Brock et al. 1987). For example, red deer (*Cervus elaphus*) hinds that had weaned a calf the previous year gave birth on average 4 days later than hinds that did not wean a calf (Clutton-Brock et al. 1983). For many mammals, late birth is associated with low fat reserves (Kruuk et al. 1999), small body size (Lunn et al. 1993) and maternal inexperience (Bowen et al. 1994). Finally, environmental conditions, such as availability and quality of food, and weather may contribute to variation in parturition date (Bunnell 1982; Cameron et al. 1993; Thompson and Turner 1982). No study, however, has investigated the simultaneous effect of maternal traits, sex of the young and yearly changes in resource availability on the timing of births or on its consequences. In addition, the consequences of birthdate on juvenile mass and growth are poorly known (Côté and Festa-Bianchet 2001; Fairbanks 1993; Green and Rothstein 1993) because data on mass and growth during early development are seldom available for wild large mammals.

We analyzed 14 years of data from a marked population of bighorn sheep to explore the proximate causes of variation in parturition date and to assess the possible consequences of birthdate, maternal characteristics and environmental conditions on individual life history. We predicted that parturition date would be heritable and genetically correlated with body mass, that heavy mothers would give birth earlier than light mothers (Festa-Bianchet and Jorgenson 1998), and that females that weaned lambs would require a longer time to ovulate and conceive, leading to later parturition the following year (Hogg et al. 1992; Hewison 1996; Iason and Guinness 1985). In addition, we expected that harsh weather during the rut may delay oestrus and consequently birthdate (Adams and Dale 1998; Pérez-Barberia and Nores 1996). We hypothesized that birthdate would affect lamb mass in mid September, because early-born lambs have more time than late-born lambs to accumulate resources before winter, and expected that lamb mass in September would be correlated with the quality of summer forage. We tested the effect of birthdate on lamb summer growth rate, to assess whether late-born lambs compensated for late birth by growing rapidly. Finally, we predicted that late birth should negatively affect survival and, as suggested by Clutton-Brock et al. (1985), we expected that late-born males would suffer greater mortality than late-born females because late birth would produce a resource shortage, which in sexually dimorphic species should have a greater effect on the development of males than of females. Because we expected substantial fitness consequences of birthdate, we wanted to know whether birthdate had genetic variation and therefore was susceptible to selection in our study population. Although we were mostly interested in the environmental variables that affect birthdate, we also tested whether birthdate was inheritable, in view of recent studies that suggested that the timing of breeding may change under the selective pressures induced by climate change (Réale et al. 2003).

Materials and methods

Study area and population

Data were collected from 1992 to 2006 at Ram Mountain, Alberta (52°N, 115°W; elevation 1,082–2,173 m), where almost all bighorns are individually marked. From late May to late September, sheep were captured several times in a corral trap baited with salt. Over 90% of lambs that survived to weaning were captured and marked in their first summer during this study. Lambs not marked during their first year were not considered in the analyses. Captured individuals were weighed to the nearest 250 g with a Detecto spring scale. Lambs gain mass linearly during summer, while adult ewes have a quadratic mass gain that can be linearized by a square-root transformation of capture date (Festa-Bianchet et al. 1996). From repeated measurements over the summer, we estimated individual growth rates and adjusted mass to 5 June and 15 September for ewes and yearlings and to 15 June and 15 September for lambs (Festa-Bianchet et al. 1996). Female reproductive status (lactating or not) was determined by udder examination during captures and field observations of lamb–ewe interactions. Ewes that had not produced lambs or whose lambs died during summer were coded as 0, while females whose lambs survived to late September [the approximate time of weaning (Festa-Bianchet 1988c)], were coded as 1. Two females whose lambs died in late August or early September were coded 1, because they bore the energetic cost of lactation during most of the summer. We considered only females aged 3 years and older (Festa-Bianchet and Jorgenson 1998) because no 2-year-old ewe lactated during this study. Since 1988, DNA sampling and molecular analyses provided paternity data (Coltman et al. 2002) for quantitative genetic analyses. We did not include in our analyses the effects of density, as over the period considered here density declined but population performance remained very poor compared to the earlier period of population increase (Pelletier et al. 2007).

Estimating individual birthdates and survival

Each year except 1993, from late May to early June, we used binoculars and spotting scopes to search for females with newborn lambs. Each lamb's age was assessed at first sighting by its size and behavior, presence of the umbilical cord and by the dark coat typical of newborns (Bérubé 1997; Geist 1971). In addition, we considered the number of days since the last sighting of the ewe without a lamb and whether or not the lamb–ewe pair was isolated from other sheep (Bérubé 1997). Ewes spend 2 or 3 days post-partum alone with their lambs before joining other females (Festa-Bianchet 1988c). When we had a range of possible birthdates, we used the average date for analyses. For 216 lambs, we estimated birthdate within ± 5 days. Birthdates were coded with May 18 as day 0. We defined the days between the first and the last birth each year as "length of the parturition season", and the time during which the first 80% of births occurred as "peak birth period" (Côté and Festa-Bianchet 2001; Rutberg 1987).

Summer survival was the proportion of lambs seen in June that were alive in mid September. Winter survival was the proportion of weaned lambs that survived to late May the following year. We were confident of our estimates of survival because for females and yearlings the yearly probability of re-sighting is over 99% (Jorgenson et al. 1997). Individuals not seen during a summer were assumed to have died, and none were re-sighted in later years.

Fecal crude protein and weather data

We measured yearly variability in the quality of summer forage by monitoring fecal crude protein (FCP), a good indicator of forage quality in our study area (Blanchard et al. 2003) that has been used in several other studies of mountain ungulates (Côté and Festa-Bianchet 2001; Leslie and Starkey 1985). We measured the percent of organic N using the Kjeldahl method. Crude protein was determined as $N \times 6.25$ (Blanchard et al. 2003). For fecal samples collected between 31 May and 18 September each year, we estimated the area under the curve described by a cubic smooth spline relating the natural logarithm of FCP to date (Blanchard et al. 2003). Weather data were obtained from the Environment Canada weather station in Nordegg, elevation 1,326 m a.s.l., about 20 km west of Ram Mountain. Following Portier et al. (1998), we used the average temperature and total precipitation from 15 May to 15 June as indicators of late spring weather. Weather conditions during the rut were defined as the average temperature and total snowfall in November and December.

Statistical analyses

Because we had repeated measurements of the same ewes for multiple years, we used mixed effects models with maternal identity (ID) and year as random terms. With a linear mixed model (LME), we tested the effects of lamb sex, maternal mass the previous autumn, maternal age and reproductive status the previous year, weather during the rut and FCP in the previous summer on birthdate. Similarly, we used LMEs to assess the effects of birthdate, maternal characters (mass previous autumn for growth rate models, mass in September for weaning mass models, age and previous reproductive status for both), FCP and spring weather (temperature and precipitations) on lamb mass on 15 September and on lamb summer growth rate. We used generalized linear mixed models to assess the effects of FCP, birthdate, lamb mass in September and sex on winter survival of lambs. We did not include winter weather in our analyses of survival because it did not appear to significantly affect lamb survival (Portier et al. 1998).

To determine which candidate models best explained the data, models were compared according to the Akaike's information criterion (AIC) statistic, and ranked according to their normalized Akaike weights (AICw). The best model had the largest AICw and the smallest AIC statistic (Burnham and Anderson 2002). Results of the model selection process are presented following the recommendations of Burnham and Anderson (2002). We used AIC corrected for small sample size (AICc; Hurvich and Tsai 1989) to select models and our data were not overdispersed. We also compared evidence ratios: the ratio of the AICw of the model with the lowest AICc score to the weight of the model of interest. AICw can be interpreted as the probability that the selected model is the best among candidate models, whereas evidence ratios measure the evidence that a model is not the best one in the set of candidate models. The larger the evidence ratio, the stronger is the evidence against a model relative to the reference model under consideration (Burnham and Anderson 2002). When candidate models differed in AICc by less than 2 units, we accepted the one with the lowest AICc as the best fit but considered other acceptable models in the discussion. All two-way interactions were investigated. However, for better clarity of the general model, only the most relevant interactions are presented in full models.

In the model selection procedure, mixed models were fitted using the maximum likelihood (ML) method, and parameters in the final model were obtained using restricted maximum likelihood estimation (REML). The significance of random terms was determined by a likelihood ratio test, calculated as $-2|(\log \text{likelihood null model} - \log \text{likelihood final model})|$, which is distributed as a χ^2 whose *df* are equal to the number of random terms (Crawley 2002). To meet normality, birthdate was square-root transformed while adjusted mass was log-transformed. Analyses were performed in R 2.4.0 (R Development Core Team 2007).

Estimating heritability of parturition date

We used a two-trait animal model to estimate both heritability and genetic correlation between parturition date and female mass during the previous autumn. We included age as a fixed term because it affects female mass (Wilson et al. 2005) and we also included all significant effects on parturition date. Year was included as a random term. Permanent environmental and maternal effects were not significant and were not included in the final model. Analyses used ASREML version 1.1 (Gilmour et al. 2002).

Results

From 1992 to 2006, we estimated birthdates for 112 males and 104 female lambs. The number of marked lambs per year ranged from 50 in 1995 to five in 2002. The timing of births varied among years, and in ten of 14 years the median birthdate was within 12 days of the first birth (Table 1). The first birth was recorded between 18 May and 2 June in all years but 2003, when lambing began 3 weeks later than the average for other years (ANOVA: year effect on birthdate, $F_{12,204} = 5.852$, $P < 0.001$). Overall, 67% of lambs were born within 2 weeks of the first birth (Fig. 1). The average duration of the lambing season was 37 days (Table 1). Average birthdate did not differ according to lamb sex ($F_{1,215} = 1.016$, $P = 0.31$) and was 8 June for males and 6 June for females.

Determinants of birthdate

We examined the effects of lamb sex, maternal age, mass and reproductive status the previous autumn, FCP and weather variables on lamb birthdate. The selected model included previous reproductive status of the mother and her body mass the previous autumn (Table 2). Successful reproduction the previous year delayed parturition date and heavier females had an earlier parturition date (Table 3). Precipitation during the rut was present in two models with $\Delta\text{AICc} < 2$ and similar evidence ratios (1.10 and 1.65) (Table 2). Therefore, parturition may be delayed following ruts with high snowfall (estimate, 0.031; 95%CI, −0.017/0.077). Birthdate was heritable and genetically correlated with maternal mass the previous year (Table 4). The average date of parturition was 3 June for multiparous mothers that did not wean a lamb the previous year, 7 June for primiparae and 10 June for ewes that had weaned a lamb the previous year.

Table 1 Descriptive statistics[a] for the birth season of bighorn sheep at Ram Mountain, Alberta, 1992–2006. *M* May, *Jn* June, *Jl* July

Year	Estimated lambs born	Lambs with known birthdate	Mean date		Median date		First birth		Last birth		Birth season (days)	SD birthdate
1992	47	25	Jn	11	Jn	14	M	26	Jl	6	41	10.86
1994	49	14	Jn	10	Jn	12	M	21	Jl	2	42	11.24
1995	68	50	M	30	M	27	M	18	Jl	7	50	9.79
1996	62	14	Jn	15	Jn	13	Jn	2	Jl	10	38	11.24
1997	43	13	Jn	12	Jn	11	M	29	Jl	12	44	14.33
1998	27	17	M	31	Jn	2	M	21	Jn	10	19	6.63
1999	27	14	Jn	5	M	30	M	28	Jl	1	34	11.45
2000	23	13	Jn	13	Jn	11	M	25	Jl	6	43	12.41
2001	20	13	Jn	15	Jn	10	M	28	Jl	16	49	16.08
2002	15	5	Jn	5	M	26	M	21	Jn	28	34	14.86
2003	11	8	Jn	13	Jn	11	Jn	7	Jn	22	15	5.33
2004	14	10	Jn	12	Jn	8	Jn	1	Jl	18	47	14.01
2005	15	10	Jn	1	M	29	M	23	Jn	20	28	8.36
2006	13	10	Jn	1	M	28	M	26	Jl	3	38	11.39

[a] Birthdates were not available for 1993

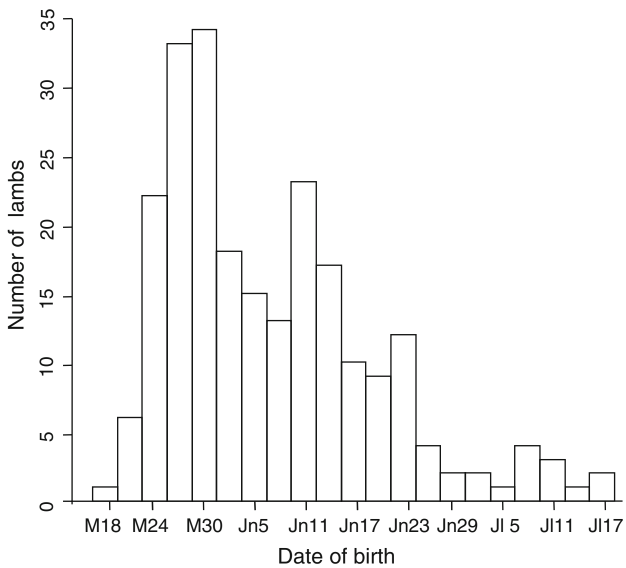

Fig. 1 Estimated dates of birth for 206 lambs in 1992–2006 at Ram Mountain, Alberta. *Bars* indicate the number of lambs born every 3 days beginning on 18 May (*M18*). *Jn* June, *Jl* July

Effect of birthdate on lamb growth rate and mass in September

Lambs of both sexes gained mass linearly through the summer (Festa-Bianchet et al. 1996). The selected model of lamb growth rate included lamb sex and previous reproductive status of the mother (Table 2). Mass gain was greater for males than for females and was lower if the mother had weaned a lamb the previous year (Table 3). Because mass gain during summer was independent of birthdate, for each day of delayed birth, males were about 210 g lighter and females about 196 g lighter in mid September. Lambs whose mothers had not weaned a lamb the previous year accumulated about 20 g more per day and were on average 2.5 kg (or about 10%) heavier at weaning than lambs whose mothers weaned a lamb the year before. The best model for lamb mass in September included birthdate, sex, previous reproductive status of the mother and maternal mass in September (Table 2). Birthdate was negatively correlated to lamb mass in June ($r = 0.60$, $P < 0.001$, $n = 101$). Late birth had a negative effect on weaning mass (Fig. 2), males were heavier than females, heavier mothers had heavier lambs, and lambs whose mother weaned a lamb the previous year were lighter than lambs whose mothers were barren the previous year (Table 3). For lamb growth rate, maternal ID (SD = 0.020, $\chi_1 = 12.2$, $P < 0.001$) accounted for 27.3% of the variance and year (SD = 0.019, $\chi_1 = 14.5$, $P < 0.001$) for 26.6%. Similarly, for weaning mass, maternal ID (SD = 0.078, $\chi_1 = 27.4$, $P < 0.001$) accounted for 38.2% of the variance and year (SD = 0.057, $\chi_1 = 14.5$, $P < 0.001$) for 20.1%.

Birthdate and survival

The selected model of lamb survival to 1 year included lamb sex, lamb birthdate, lamb mass in September and the interaction between sex and birthdate (Table 2). Heavier lambs in September had a higher survival probability and late birth had a negative effect on the survival of male lambs (Fig. 3, Table 3). Maternal ID (SD < 0.01; $\chi_1 = 0.01$; $P = 0.96$) and year (SD = 0.361; $\chi_1 = 0.75$; $P = 0.28$) did not affect lamb survival. The addition of lamb mass in September slightly improved a model of survival determined by birthdate, lamb sex and their interaction (Table 4; ΔAICc < 2 and similar evidence ratio, 1.00 and 1.66). Including lamb mass in the model led to a reduction in the standardized estimates of the effects of birthdate (−0.57 without and −0.25 with lamb mass) and the birthdate × sex interaction (0.64 without and 0.46 with lamb mass) suggesting that the effect of birthdate on survival was mostly mediated through a decrease in body mass.

Discussion

In strongly seasonal environments, synchrony in parturition may be selected for by the short time available to juveniles to attain sufficient body mass to survive the winter (Festa-Bianchet 1988a; Green and Rothstein 1993). Four of our results have evolutionary consequences. First, parturition date is heritable, genetically correlated with body mass and affected by previous reproductive success; second, late-born lambs cannot compensate for a shorter time to accumulate resources before winter and are lighter at weaning; third, late birth had a weak negative effect on winter survival; fourth, the negative effects of late birth on mass at weaning and survival were stronger for male than for female lambs.

A complex interaction of environmental and genetic parameters affected birthdate, producing variation among years and among females. Parturition date is heritable and heavy maternal mass in September is genetically correlated with early parturition the following spring. Successful previous reproduction and heavy snow during the rut delayed parturition date. In the Ram Mountain population, ewes that wean a lamb one year suffer a decrease in weaning success the following year, and the cost of reproduction is greater for light than for heavy ewes (Festa-Bianchet et al. 1998). Females that nursed a lamb until September may be in poorer condition than females that had not lactated during the previous year, and may require more time to attain oestrus, as has been reported for other ungulate populations (Clutton-Brock et al. 1982; Green and Rothstein 1993; Hogg et al. 1992). Several studies also report that deep snow lowers the foraging efficiency of mountain ungulates

Table 2 Model selection with Akaike's information criterion corrected for small sample size (*AICc*) for the determinants of parturition date, lamb growth rate, mass in mid September and survival for bighorn sheep on Ram Mountain, Alberta, 1992–2006. Full and null models are presented with the three best models considered for each analysis. Year and mother identity (ID) were included in all models as random effects. Selected models are shown in *bold*. *K* Number of parameters in each model, *BD* birthdate, *S* sex, *LMJ* lamb mass in June, *LMS* lamb mass in September, *MMPF* mother mass previous fall, *MMS* mother mass in September, *A* age, *PRS* previous reproductive status, *FCP* fecal crude protein, *PFCP* previous year FCP, *TR* mean temperature during rut (November–December), *PR* total precipitation during rut, *TS* mean temperature in spring (May–June), *PS* total precipitation in spring

	K	AICc	ΔAICc	w_i	Evidence ratio
Parturition date[a] ($n = 185$)					
PRS + MMPF + A+S + PFCP + TR + PR	11	633.63	3.87	0.05	6.91
Null model (random effects only)	4	631.64	1.88	0.13	2.56
PRS + MMPF	**6**	**629.77**	**0.00**	**0.33**	**1.00**
PRS + MMPF + PR	7	629.95	0.19	0.30	1.10
PRS + MMPF + S+TR + PR	9	630.77	1.00	0.20	1.65
lambs growth rate[a] ($n = 124$)					
BD + S+LMJ + PRS + MMPF + A+FCP + TS + PS + BD:LMJ	14	−501.90	8.93	0.01	86.76
Null model (random effects only)	4	−500.54	10.28	0.00	170.70
S + PRS	**6**	**−510.82**	**0.00**	**0.54**	**1.00**
S + LMJ + PRS	7	−509.32	1.50	0.25	2.12
BD + S+LMJ + PRS	8	−508.86	1.96	0.20	2.66
Lambs mass in September[a] ($n = 138$)					
BD + S+MMS + PRS + A+FCP + TS + PS	12	−189.75	8.25	0.01	61.86
Null model (random effects only)	4	−124.28	73.72	0.00	>1000
BD + S+MMS + PRS	**8**	**−198.00**	**0.00**	**0.51**	**1.00**
BD + S+MMS	7	−197.28	0.73	0.36	1.44
BD + S+MMS + FCP	8	−195.09	2.92	0.12	4.30
Winter survival of lambs[b] ($n = 149$)					
S + BD + LMS + FCP + S:BD + S:LMS + BD:LMS	11	208.64	4.07	0.06	7.65
Null model (random effects only)	4	212.71	8.14	0.01	58.68
S + BD + LMS + S:BD	**8**	**204.57**	**0.00**	**0.43**	**1.00**
S + BD + S:BD	7	205.58	1.01	0.26	1.66
S + BD + LMS	7	205.68	1.11	0.25	1.75

[a] Data fitted with ML linear mixed models

[b] Data fitted with generalized linear mixed model with a binomial distribution

and increases physiological stress (Huber et al. 2003; Saltz and White 1991). Both effects could delay oestrus.

Negative correlations between birthdate and juvenile mass have been reported for several ungulates (Côté and Festa-Bianchet 2001; Kruuk et al. 1999; Green and Rothstein 1993; Gaillard et al. 1993), and for other mammals (Boyd and McCann 1989; Rieger 1996). In our study, birthdate explained almost 30% of the variability in lamb mass in September. Our model selection procedure suggested that maternal mass in September was positively correlated with lamb mass in September, but the correlation appeared very weak, as previously reported (Festa-Bianchet and Jorgenson 1998). Contrary to our prediction, however, mother's age did not affect lamb mass at weaning, suggesting that direct maternal effects on lamb mass at weaning are weak. The lighter mass of late-born lambs was apparently mostly due to the shorter period available for mass gain, because birthdate had no effect on summer growth rates. Late-born lambs could not compensate for their initial disadvantage, contrary to what has been reported for bison (Green and Rothstein 1993). Male lambs had a faster growth rate than females and were about 7% heavier at weaning. The negative effects of late birth on mass were greater for males than for females, because being a small female does not preclude reproduction, while being a small male greatly decreases the probability of access to females (Andersson 1994; Coltman et al. 2002; Clutton-Brock et al. 1988).

Late birth decreased survival to 1 year, particularly for males. We found no effect of birthdate on survival of female lambs, and we suspect that survival may decrease only for female lambs that are born extremely late. Our

Table 3 Parameter estimates of fixed effects for selected models from Table 2 for the determinants of parturition date, lamb growth rate, mass in mid September and survival over the winter for bighorn sheep on Ram Mountain, Alberta, 1992–2006. Year and mother ID were included in all models as random effects. Male lambs and 'fail to wean lamb previous year' were considered as references in analyses. *CI* Confidence interval

	Estimates	95% CI	
Parturition date[a] ($n = 185$)			
Intercept	13.150	2.688	23.065
Previous reproductive status (lamb weaned)	0.359	−0.045	0.747
Mother mass previous fall	−2.103	−4.461	0.335
Lamb growth rate[a] ($n = 124$)			
Intercept	0.225	0.210	0.241
Lamb sex (female)	−0.015	−0.024	−0.005
Previous reproductive status (lamb weaned)	−0.015	−0.026	−0.004
Lambs mass in September[a] ($n = 138$)			
Intercept	1.028	−0.140	2.663
Birthdate	−0.062	−0.081	−0.049
Lamb sex (female)	−0.066	−0.099	−0.030
Previous reproductive status (lamb weaned)	−0.034	−0.078	0.005
Mother mass in September	0.592	0.210	0.865
Winter survival of lambs[b] ($n = 149$)			
Intercept	−8.135	−17.674	0.938
Sex (female)	−0.124	−2.398	2.158
Birthdate	−0.178	−0.582	0.198
Lamb mass in September	2.529	0.030	5.181
Birthdate × sex (female)	0.331	−0.201	0.877

[a] Analyses used restricted maximum likelihood linear mixed models

[b] Analyses used generalized linear mixed model with a binomial distribution

Table 4 Heritability (h^2; on the diagonal), phenotypic (r_P; below the diagonal) and genetic correlations (r_A; above the diagonal) of parturition date and mass the previous September for bighorn ewes at Ram Mountain, Alberta, 1992–2006. SEs are given for each value; significant values are in *bold*

	Parturition date	Mass previous fall
Parturition date	**0.13 (0.06)**	**−0.24 (0.07)**
Mass previous fall	**−0.55 (0.22)**	**0.67 (0.06)**

sample included very few females born after 25 June (Fig. 2). The negative relationship between birthdate and survival was likely mediated by the effect of birthdate on mass at weaning. In sexually dimorphic mammals and birds, young males suffer greater mortality than young females under difficult conditions (Clutton-Brock et al.

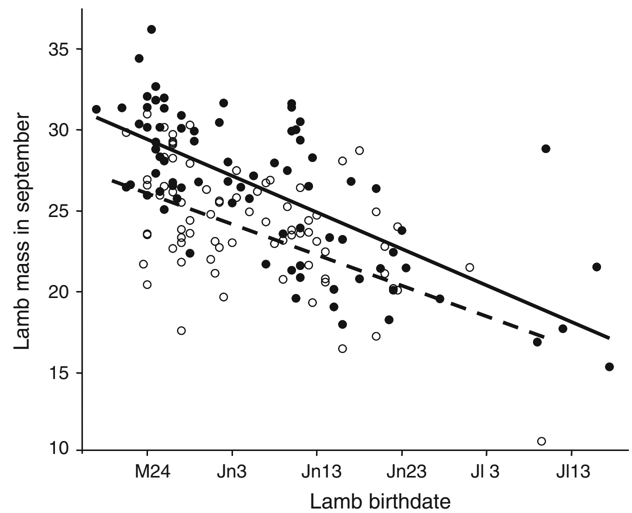

Fig. 2 Mass adjusted to 15 September according to birthdate for bighorn lambs in 1992–2006 at Ram Mountain, Alberta. Males are represented by *solid circles* and *solid line*, females by *open circles* and *dashed line*

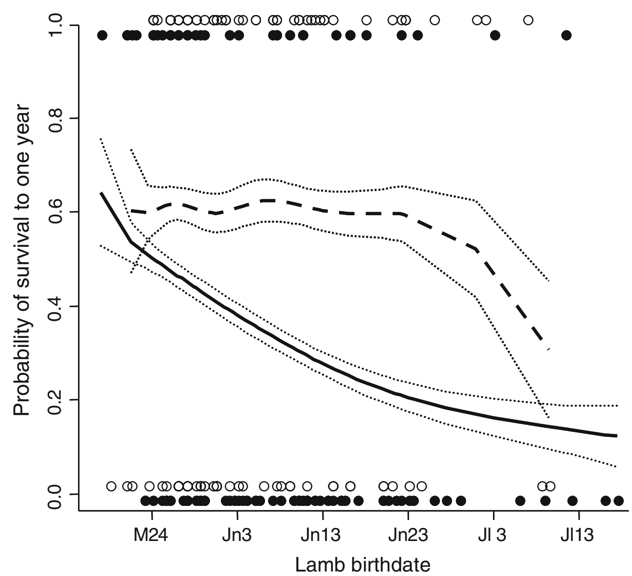

Fig. 3 Survival to 1 year according to birth date and sex for bighorn lambs in 1992–2006 at Ram Mountain, Alberta. Observations for males are represented by *full circles*, for females by *open circles*. *Solid* and *dashed lines* represent smooth-splines of predicted values (log odds) of the logistic regression model of survival (see Table 3) for males and females, respectively. *Dotted lines* show confidence intervals (twice the SE)

1985). The higher susceptibility of males to food shortage is associated with their faster growth rate, greater nutritional requirements and need of greater maternal care compared to females (Bérubé et al. 1996; Bowen et al. 2001; Clutton-Brock et al. 1985). Apparently, males invest more in growth and less in maintenance than females. As a consequence males need more resources than females to assure both their growth and their survival. Because of the short growing season, in mountain ungulates late-born individuals appear unable to obtain sufficient body growth and fat accumulation (Côté and Festa-Bianchet 2001; Festa-Bianchet 1988a). Late birth may act similarly to a food shortage: male lambs cannot obtain a sufficient amount of food during summer to survive the winter.

During our study, 80% of lambs were born by 14 June, which is later than in other populations of mountain ungulates in Alberta [for bighorn sheep, 80% of lambs born by 3 June (Festa-Bianchet 1988a); for mountain goats, 80% of parturitions by 31 May (Côté and Festa-Bianchet 2001)]. At Ram Mountain, the birth peak was less pronounced than in other bighorn populations (Festa-Bianchet 1988a; Hass 1997) or in other ungulates (Côté and Festa-Bianchet 2001; Fairbanks 1993). Only 47% of lambs were born before 1 June, fewer than the 71% reported by Festa-Bianchet (1988a) at Sheep River, 200 km south of Ram Mountain. Parturitions were later during this study than during earlier years at Ram Mountain. Even though we have no data on estimated birthdates, before 1990 it was exceptional to capture a pregnant ewe in late May, while in later years many ewes were pregnant at their first capture in late May or early June (Bérubé 1997). During this study lambs were also 14% lighter at weaning (partly because of late birthdate) than before 1990 (Festa-Bianchet et al. 1997). In addition, age of primiparity increased (Jorgenson et al. 1993), suggesting that the population was experiencing poor conditions. During this study, however, birthdate was independent of forage quality as measured by FCP. The increase in occurrence of late-born lambs at Ram Mountain over the last decade may be a sign that the population is affected by factors other than environmental harshness, including, possibly, loss of genetic variability or indirect selection. The selection for lower horn size and body mass induced by trophy hunting (Coltman et al. 2003) on Ram Mountain since 1972 could have led to late births through the strong genetic correlations between ewe mass and ram mass and horn size (Coltman et al. 2005) and between ewe mass and parturition date.

We found a strong fitness cost of previous reproduction: on average, females that had weaned a lamb the year before gave birth a week later than barren females. Late birth led to reduced weaning mass and lower winter survival, especially for male lambs. This result is consistent with earlier reports of fitness costs of reproduction in bighorn sheep ewes (Bérubé et al. 1996; Festa-Bianchet et al. 1998; Hogg et al. 1992). The negative effects of birthdate on weaning mass and winter survival could bias analyses of maternal care, because weaning mass varies with birthdate, in addition to maternal expenditure and resource abundance. Ignoring variation in parturition date could affect estimates of maternal reproductive effort. Festa-Bianchet and Jorgenson (1998) suggested that maternal effort decreased at high population density, because mass gain by lambs over the summer and weaning mass decreased with increasing density while mass gain and mid September mass by lactating ewes did not. Environmental variation leading to later parturition date, and consequently to a lower weaning mass and a lower survival, could be interpreted as a decrease in reproductive effort if birthdates are not taken into account. It is therefore important that the effects of birthdate on life history traits are included in the analysis of reproductive effort, selection and evolution of life history traits.

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