

Determinants and consequences of age of primiparity in bighorn ewes

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Because variation in age of first reproduction can have major effects on individual fitness and population dynamics, it is important to understand what maintains that variability. Although early primiparity is assumed to be costly, it is sometimes associated with high lifetime reproductive success. We used a long-term study on bighorn sheep *Ovis canadensis* to determine what variables affect age at first reproduction, investigate the impact of primiparity on body resources and quantify the reproductive performance of primiparous ewes. We then examined the consequences of delayed primiparity on adult body mass, longevity and lifetime reproductive success. Environmental conditions during early development, body mass as a yearling, genotype and maternal effects affected age of primiparity. Primiparous ewes lost more mass in winter and gained less mass in summer than multiparous ewes. Small yearling ewes that postponed reproduction attained similar adult mass than heavy yearling ewes who reproduced at a younger age. Early primiparity did not reduce longevity and was positively associated with lifetime reproductive success. Starting to reproduce as soon as possible appears to maximize fitness of females. When early life conditions are unfavorable, however, delayed primiparity allows greater body growth and likely maximizes survival. The combination of a conservative reproductive strategy and maternal effects on age of primiparity may partly delay population recovery following density-dependent declines.

Because of tradeoffs between current reproduction and subsequent reproductive potential, individuals are expected to reproduce at a particular time as a function of their condition (Stearns 1992, Roff 2002). In species that can reproduce before completing body growth, the timing of the first reproduction can have major fitness consequences (Swain et al. 2007). Reproducing too early may decrease longevity and lifetime reproductive success (Descamps et al. 2006). On the other hand, a delay in primiparity increases the chance to die before any reproduction and may shorten the reproductive lifespan (Blomquist 2009). Early reproduction may also compromise growth and reduce asymptotic mass (Stamps et al. 1998). Delayed primiparity would only be selected for if the resulting increase in future reproductive success was on average higher than the loss from the missed reproductive opportunity (Partridge and Harvey 1988). Thus, individuals in good condition are predicted to start to reproduce earlier than individuals in poor condition (Descamps et al. 2006). Because age of primiparity is an important life-history trait, it has been studied in a wide diversity of taxa, including birds (Cooper et al. 2009, Aubry et al. 2009), terrestrial mammals (Neuhaus et al. 2004), marine mammals (Hadley et al. 2006), fish (Swain et al. 2007) and reptiles (Bonnet et al. 2002). No study of vertebrates, however, has compared the causes and consequences of primiparity over a wide range of environmental conditions while taking into account individual differences in mass and the heritability, including

possible maternal effects, of this important life-history trait. Here, based on 35 years of monitoring of marked bighorn sheep *Ovis canadensis* females over a period when environmental conditions changed drastically, we analyze the determinants of age of primiparity, the direct short-term costs of primiparity and the long-term fitness consequences of variation in age at first reproduction.

Although early primiparity is typically assumed to be costly, many studies failed to detect any associated growth costs and some found positive correlations between early maturation and subsequent mass (Reimers 1983, Green and Rothstein 1991, Gaillard et al. 1992, Jorgenson et al. 1993). Some studies of wild mammals found that early primiparity lowered survival or subsequent reproductive success (Huber 1987, Miura et al. 1987, Reiter and Leboeuf 1991). Other studies, however, found that precocious breeders had the same or better subsequent survival and reproductive success than females that first bred at a later age (Ozoga and Verme 1986, Festa-Bianchet 1989, Green and Rothstein 1991, King et al. 1991, Hamel et al. 2008). Individual heterogeneity limits our ability to detect costs of reproduction (van Noordwick and de Jong 1986, Reznick et al. 2000). Costs of reproduction are expected from energetic tradeoffs, but if individuals differ in reproductive potential, an analysis at the population level may not find any costs of reproduction (Roff 2002). In female ungulates, individual variability often hides the costs of reproduction as some individuals always

perform better than others (Hamel et al. 2008). Thus, it is important to account for individual heterogeneity when analysing costs of reproduction (Weladji et al. 2008).

An important goal of evolutionary biology is to estimate individual variation in fitness-related traits then partition it into its genetic and environmental components. Genetic components of variance determine the rate at which traits may respond to selection, while environmental components provide an indication of phenotypic plasticity (Falconer and Mackay 1996). Maternal effects are a potentially important source of environmental variation, especially in mammals (Mousseau and Fox 1998). Maternal effects include pre- and postnatal influences, mainly nutritional, of the mother on her offspring. For instance, larger mothers may produce larger offspring because they had more resources at conception, independently of genotype. Variables that affect early development and juvenile mass, including maternal effects and environmental conditions (Lindstrom 1999) also affect age of first reproduction. Hence, we predicted that maternal and cohort effects would affect the age of primiparity.

Body mass is an important determinant of age at primiparity. A minimum mass may be required to sustain first reproduction (Jorgenson et al. 1993, Sæther and Heim 1993). If early maturation depletes body resources, a female will only reproduce after accumulating enough resources to bear the cost of primiparity and continue her body growth. An earlier investigation of our study population of bighorn sheep, however, found wide overlap in mass of primiparous and nulliparous young females, contradicting the 'threshold mass hypothesis' (Festa-Bianchet et al. 1995) and suggesting that genetic, maternal or environmental effects may be more important than mass alone. Population density can strongly affect age at primiparity (Gaillard et al. 2000a), most likely because low resource availability at high density reduces the ability to recover the somatic costs of reproduction. An increase in age of primiparity is often the first detectable symptom of density-dependence in ungulate populations (Gaillard et al. 2000a). We thus expected that high population density in early life would delay primiparity.

Few determinants of age at primiparity other than body mass have been identified for most large mammals. In bighorn sheep, mass as a yearling and population density affected age of primiparity but maternal and genetic effects were not evaluated (Jorgenson et al. 1993). Age of primiparity had no apparent effects on lifetime reproductive success or on longevity (Festa-Bianchet et al. 1995) but the consequences of variation in age of primiparity on adult mass are unknown. The somatic costs of primiparity may vary with juvenile mass, environmental conditions during early development and maternal condition. Previous research on primiparity in bighorn ewes focused mostly on reproduction of 2-year old females (Jorgenson et al. 1993, Festa-Bianchet et al. 1995). Compared to those earlier studies, 15 more years of data provided us with both a wider variation in population density and in age of primiparity, ranging from 2 to 7 years.

Few studies have assessed the additive genetic basis of age of primiparity in the wild, and none estimated maternal effects. Age of primiparity is heritable in rhesus macaques *Macaca mulata*; $h^2 = 0.13 \pm 0.03$ (Blomquist 2009); and in red deer *Cervus elaphus*; $h^2 = 0.29 \pm 0.12$ (Kruuk et al. 2000). For bighorn sheep at Ram Mountain, Coltman et al. (2005)

reported a nonsignificant additive genetic variation of age of primiparity using an 'animal' model ($h^2 = 0.16 \pm 0.15$) which, however, did not account for density, body mass, maternal and cohort effects. Using a larger sample size and a deeper pedigree, we re-evaluated the additive genetic basis as well as the environmental determinants of age of primiparity in this population.

We explore three main questions. What are the determinants of primiparity? What are the somatic costs of primiparity? And what are the effects of variation in age of primiparity? Based on earlier research on wild ungulates (Green and Rothstein 1991, Jorgenson et al. 1993), we predicted earlier primiparity for females that were heavy as yearlings. We also estimated the additive genetic and maternal environmental variance components of age of primiparity. Based on earlier results by Coltman et al. (2005) on a smaller sample, we expected to find low but significant heritability. To evaluate how first reproduction may affect growth and to estimate how age may affect a female's success during her first reproductive attempt, we compared primiparous ewes with nulliparous and multiparous ones of the same age. Finally, we quantified the consequences of variation in age of primiparity on adult mass, longevity and lifetime reproductive success. Based on earlier work by Festa-Bianchet et al. (1995) suggesting low costs of early maturation, we expected variability in primiparity to be based on individual reproductive potential, so that subsequent growth rate, lifespan and lifetime reproductive success would be independent of age of primiparity.

Methods

Study area and population

Bighorn sheep on Ram Mountain (52°8'N, 115°8'W, elevation 1082 to 2173 m), Alberta, Canada, were monitored from 1971 to 2008. Between May and September, sheep are captured several times in a corral trap baited with salt (Jorgenson et al. 1993). Adults are marked with visual collars or plastic ear tags. Nearly all ewes born since 1972 were of known age because they were first captured as lambs or yearlings. At each capture, we recorded body mass (kg), and classified ewes as lactating or not by examining their udder. Ewes never produce more than one lamb per year. Lamb-ewe matches were established through repeated field observations of suckling. We classified ewes as lactating if their lamb was alive. Yearly reproductive success of individual ewes was measured by lamb survival to one year, which included both weaning success (lamb survival to September 15th) and lamb overwinter survival. Lifetime reproductive success was estimated as the total number of lambs weaned. Because resighting rate of adult females was over 99% (Loison et al. 1999), estimates of longevity based on the last observation of an individual are accurate.

Since 1988, paternity was determined using molecular techniques, which also confirmed our maternity assignments (Coltman et al. 2002, Poissant et al. 2008). By 2008, the Ram Mountain pedigree included 791 maternal and 461 paternal links, involving 1017 sheep since 1971. Every year, we classified each female as 'nulliparous' (never reproduced),

‘primiparous’ (first reproduction) and ‘multiparous’ (reproduced for at least the second time). We used the number of adult females (≥ 2 years old) in June each year as an index of population density (Festa-Bianchet and Jorgenson 1998).

Using repeated measurements of the same individual each summer, we adjusted body mass to spring (5 June, except for lambs whose mass was adjusted to 15 June as some were born in early June) and fall (15 September) for each sheep. We used linear mixed models with a restricted maximum likelihood (REML) method to adjust mass by fitting it as a function of date with 25 May as day 1 (Pelletier et al. 2007, Martin and Pelletier 2011). Lambs and yearlings gained mass linearly during summer. A square root transformation of date linearized the relationship between mass and date for adult ewes (Festa-Bianchet et al. 1996). We included individual identity (as an intercept) and the interaction between identity and date (as a slope representing individual mass gain rate) as random effects. We fitted separate linear mixed models for each year and used the predicted values of individual intercepts and slopes (provided by BLUPs) to adjust individual mass. Despite potential biases associated with BLUPs (Hadfield et al. 2010), the mixed-model approach provides a more accurate adjustment of body mass than a linear regression for each individual, especially for those only weighed twice in a summer (Martin and Pelletier 2011). Summer mass gain was the difference between an individual’s mass in September and in June. Relative summer mass gain was gain corrected for mass in spring (Pelletier et al. 2007).

Statistical analyses

Determinants of age of primiparity

To study determinants of age of primiparity, we included 152 ewes for which both age of primiparity and mother’s identity were known. We fitted an animal model including each ewe’s mass as a yearling in mid-September, population density experienced as a yearling and their interactions as fixed effects. We refer to the number of adult ewes in June when each ewe was one year old as ‘density as yearling’, an index of environmental conditions during early development. An animal model is a linear mixed-model where individuals are linked by a pedigree, so that the variance can be decomposed into quantitative genetic parameters (Kruuk 2004). The non-normal distribution of age at primiparity induced mis-behaving residuals and violated several assumptions of the restricted maximum likelihood (REML) method to fit an animal model (Kruuk 2004). Therefore, we instead adopted a Bayesian approach using ‘MCMCglmm’ (Hadfield 2010, Wilson et al. 2010). MCMCglmm is an R package that implements Markov chain Monte Carlo (MCMC) routines for fitting multi-response generalized linear mixed model (Hadfield 2010). Based on MCMC sampling, fixed effects whose 95% credible intervals excluded zero were considered significant (Sorensen and Gianola 2007, Wilson et al. 2010). We decomposed the total phenotypic variance (V_p) into its additive genetic (V_A), maternal (V_M), year of birth (V_{YOB}) and residual (V_R) components. Maternal effects included both maternal environmental and maternal genetic effects and controlled for shared environment by daughters and mothers. Narrow sense heritability (h^2) and other ratios were calculated by dividing the appropriate variance compo-

nents by V_p (i.e. V_A/V_p for h^2). Because variance component are constrained to be positive, we assessed the significance of additive genetic and maternal effects based on the deviance information criterion (DIC) comparing models with and without a random effect (Wilson et al. 2010). The model with the lowest DIC is considered to have the best fit among candidate models (Spiegelhalter et al. 2002). A difference greater than 10 is usually considered as strong evidence in favour of the model with lower DIC. For all models fitted with MCMCglmm, we used weak uninformative inverse-wishart priors. To achieve a good mixing of MCMC chains, we ran 520 000 iterations with a burn-in period of 20 000 and a thinning interval of 500 for each model. Details about the Bayesian approach used and the MCMCglmm function are provided in Hadfield (2010) and Wilson et al. (2010).

To avoid pseudo-replication, we used linear mixed models with ewe identity and year as random effects when necessary. Significance of random effects was estimated using a log-likelihood ratio test (LRT) with 1 degree of freedom (Pinheiro and Bates 2000). Following Whittingham et al. (2006), we report full models including linear non-significant terms. We tested all two-ways interactions but report only significant ones (Engqvist 2005). For all models, excluding non-significant parameters provided similar results.

Direct costs of primiparity

Because most ewes start to reproduce before completing body growth, mass change of primiparous females should be compared with that of reproductive and non-reproductive females of the same age. To examine the direct effects of primiparity, we therefore restricted our analysis to ewes aged 3 or 4 years, which included individuals in all three reproductive states. We included female identity and year as random effects. We compared mass changes of nulliparous, primiparous and multiparous young ewes. First, we assessed the impact of first gestation by estimating mass loss during winter as a function of age, mass the previous September (about 2.5 months before conception), parity status and population density. We then evaluated the somatic costs of first lactation by estimating summer mass gain as a function of age, post-parturition mass in June, parity and population density.

To evaluate the success of first reproduction, we compared mass and survival to one year of lambs born to primiparous and multiparous ewes. We fitted a linear mixed model of lamb mass in September and reproductive success (logistic response) as a function of parity (primiparous vs multiparous), lamb sex, maternal age, maternal mass the previous September and population density.

Consequences of delayed primiparity

To evaluate how delayed primiparity affected body growth, we fitted a model of ewe mass in September as a function of age, age of primiparity, their quadratic terms and their interactions as fixed effects. The inclusion of quadratic terms for age and age of primiparity allows to model the asymptotic growth of sheep between 1 and 7 years. Ewe identity and year were fitted as random effects. Because bighorn ewes complete body growth by about 6 years of age (Festa-Bianchet et al. 1996), we modelled mass from ages one to six. To verify that apparent mass changes were not due to mass-related

differential mortality, we fitted a logistic model of survival to six years old as a function of body mass as yearling. To estimate the fitness consequences of delayed primiparity, we fitted models of longevity and lifetime reproductive success (natural log+1 transformed) as a function of age of primiparity, mass as a yearling and density as yearling. Longevity was also added as a fixed effect in the model of lifetime reproductive success. To test for directional and stabilizing selection, we evaluated linear and quadratic effects of age of primiparity on both fitness proxies. Year of birth was fitted as a random effect to prevent any cohort bias. We excluded individuals born after 2000, to ensure that we had complete lifetime records. Only 4 ewes (average age 12 years) born before 2000 were alive in September 2008. All statistical analyses used R 2.10.0 (R Development Core Team 2010).

Results

Determinants of age of primiparity

Yearling mass (estimate = -0.13 , CI = $-0.19 - -0.06$, $p < 0.001$), density as yearling (estimate = -0.10 , CI = $-0.09 - -1 \times 10^{-3}$, $p = 0.03$) and their interaction (estimate = 1.52×10^{-3} , CI = $3.84 \times 10^{-4} - 2.48 \times 10^{-3}$, $p = 0.005$) affected age of first reproduction. Among females that experienced low population density as yearlings, those that were heavier as yearlings reproduced at a younger age than lighter ones (Fig. 1). When density was high, however, yearling mass did not affect age of first reproduction (Fig. 1). The inclusion of additive genetic, maternal environment and year of birth random effects improved the model fit substantially (Table 1). Age of first reproduction was heritable ($b^2 = 0.17$, CI = $0.03 - 0.43$), and was influenced by both maternal effects ($m^2 = 0.12$, CI = $0.03 - 0.40$) and year of birth ($YOB^2 = 0.34$, CI = $0.11 - 0.53$).

Direct costs of primiparity

Mass loss in winter for females aged 3 and 4 years was influenced by their mass the previous September and their parity, but not by age and density (Table 2). As reported by Pelletier et al. (2007), heavy females lost more mass than light females. Once the effect of mass in September was accounted for, multiparous females lost, on average, 1.5 kg more (about 2% of September mass, and 13% of average winter mass loss) than nulliparous ones, while primiparous females lost 1.7 kg (95% CI: $-2.63 - -0.70$, $p = 0.02$) more than multiparous and 3.2 kg more than nulliparous females, about 27% of average winter mass loss (Table 2, Fig. 2a). Female identity was not a significant random effect ($\sigma^2 < 0.01$, proportion of variance (pov): < 0.01 , LRT < 0.01 , $p = 0.99$) but year was ($\sigma^2 = 3.75$, pov: 0.28, LRT = 58.37, $p < 0.001$).

Summer mass gain was independent of density and age but it was reduced by primiparity (Table 2). Primiparous females gained 0.8 kg less than nulliparous and 1 kg (about 6% of average summer mass gain for this age group) less than multiparous females (Table 2, Fig. 2b). Females mass in June was negatively correlated with summer mass gain (Table 2). Both female identity and year explained some variance in summer mass gain (identity: $\sigma^2 = 1.04$,

pov: 0.11, LRT = 6.55, $p = 0.01$; year: $\sigma^2 = 4.23$, pov: 0.46, LRT = 123.08, $p < 0.001$).

Lamb mass at weaning was affected by mother's parity, age and mass in September before conception (Table 3). Heavier females produced heavier lambs, while older females produced lighter lambs, once parity and lamb sex were controlled for. Lambs of primiparous females were 2 kg (or about 8%) lighter than those of multiparous ones (Table 3, Fig. 2c). Female identity was not a significant random effect ($\sigma^2 = 3.93$, pov: 0.35, LRT = 2.27, $p = 0.13$) but year was ($\sigma^2 = 4.18$, pov: 0.37, LRT = 4.15, $p = 0.04$).

Lamb survival to one year was influenced by population density but was independent of sex, maternal mass before conception, ewe age or primiparity (Table 3, Fig. 2d). Neither female identity nor year affected lamb survival to one year (identity: LRT < 0.01 , $p = 0.99$; year: LRT = 1.47, $p = 0.22$).

Consequences of delayed primiparity

Ewe body mass from 1 to 6 years was influenced by age, age of first reproduction, their quadratic terms and interactions (Table 4, Fig. 3). As yearlings, females with a later age of primiparity were smaller, but by age 6 mass was independent of age of primiparity (Fig. 3). Female identity and year were both significant (Table 4). Survival to 6 years of females included in this sample was high (85%; of 203 yearlings only 32 died) As yearlings, females that survived to 6 years were 0.68 ± 1.09 kg heavier than those that did not, but the difference was not significant ($n = 203$, slope: -0.021 , SE: 0.035, $Z = -0.622$, $p = 0.53$).

Longevity was positively related to yearling mass but was independent of density as a yearling (Table 5). Inversely, lifetime reproductive success was negatively related to density as yearling but independent of yearling mass (Table 5). Age of

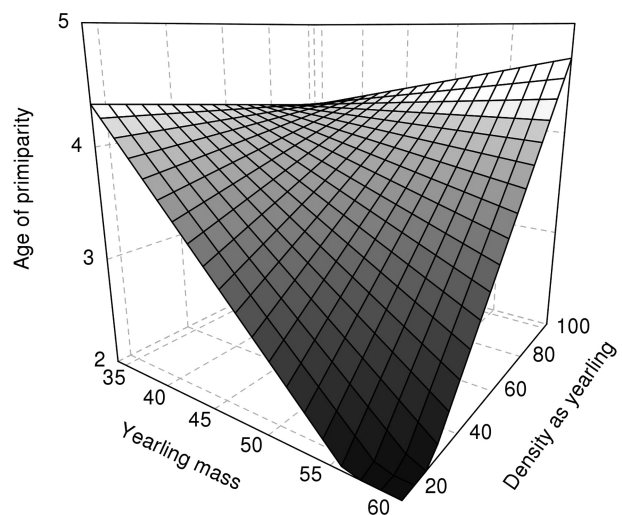


Figure 1. Prediction of age of primiparity according to yearling mass, density as yearling and their interaction for bighorn ewes at Ram Mountain, Alberta. The figure is based on the model in Table 4. Terms plotted in the figure explain 30% of the variance in age of primiparity.

Table 1. Heritability and variance components (with credible intervals) of age at first reproduction in bighorn ewes at Ram Mountain, Alberta, estimated with a Bayesian animal model for 203 ewes born in 1973–2006. Yearling mass, density as a yearling and their interaction were included as fixed effects.

Model	V_A^a	V_M	V_{YOB}	V_P^b	h^2^c	m^2	YOB^2	DIC ^d
1. $V_P = V_{YOB} + V_R$	–	–	0.229 (0.09–0.52)	0.643 (0.49–0.95)	–	–	0.368 (0.20–0.60)	318.24
2. $V_P = V_A + V_{YOB} + V_R$	0.138 (0.04–0.36)	–	0.235 (0.08–0.50)	0.672 (0.49–0.94)	0.209 (0.06–0.52)	–	0.361 (0.20–0.59)	272.52
3. $V_P = V_A + V_{ME} + V_{YOB} + V_R$	0.096 (0.02–0.31)	0.084 (0.02–0.28)	0.182 (0.06–0.46)	0.659 (0.50–0.95)	0.169 (0.03–0.43)	0.116 (0.03–0.40)	0.341 (0.11–0.53)	238.08

^avariance components: V_A = additive genetic; V_M = maternal; V_P = phenotypic; V_R = residual; V_{YOB} = year

^bphenotypic variance conditional on fixed effects. Raw phenotypic variance estimated directly from the data was 0.932

^cvariance components as a proportion of the phenotypic variance; h^2 = heritability; m^2 = maternal effects; YOB^2 = year effects

^ddeviance information criterion. Model with the lowest DIC is considered as the best fitting model

primiparity did not seem to affect longevity but had a negative linear effect (directional selection) on lifetime reproductive success (Table 5). Ewes that started to reproduce early had higher reproductive success. Quadratic effects of age of primiparity (stabilizing selection) were not significant (longevity: 0.05, CI = –0.32 – 0.40, $p = 0.80$; reproduction: –0.027, CI = –0.081 – 0.028, $p = 0.34$). Longevity had a positive effect on lifetime reproductive success (Table 5). Dropping longevity from the lifetime reproductive success model did not change the age of primiparity effect. Year of birth explained part of the variance in both longevity ($\sigma^2 = 2.23$, pov: 0.16, LRT = 12.18, $p < 0.001$) and lifetime reproductive success ($\sigma^2 = 0.09$, pov: 0.25, LRT = 9.49, $p < 0.001$).

Discussion

Previous research on the causes and consequences of variation in age of primiparity in bighorn sheep focused on reproduction by 2-year-old ewes. Mass and density interacted to

Table 2. Estimates from linear mixed models of effects of parity, age, initial body mass and density on mass variation (winter loss and summer gain) of bighorn ewes aged 3 or 4 years at Ram Mountain, Alberta. Ewe identity and year were fitted as random effects. Parameters with a significant effect are in bold.

Fixed effects	Estimates	95% CI		p-value
Winter mass loss (n = 380, from 200 females over 33 years, $R^2 = 0.54$)				
(intercept)	11.74	7.62	15.50	<0.001
parity^a				
primiparous	–3.22	–4.22	–2.20	<0.001
multiparous	–1.48	–2.77	–0.33	0.013
age	–0.84	–1.79	0.15	0.097
mass in September	–0.30	–0.37	–0.23	<0.001
density	0.01	–0.01	0.04	0.26
Summer mass gain (n = 382, from 201 females over 34 years, $R^2 = 0.59$)				
(intercept)	24.31	20.80	26.78	<0.001
parity^a				
primiparous	–0.80	–1.45	0.00	0.026
multiparous	0.19	–0.61	1.16	0.68
age	–0.13	–0.81	0.47	0.67
mass in June	–0.13	–0.18	–0.07	<0.001
density	–0.02	–0.04	0.00	0.14

a ‘nulliparous’ (ewes that had never reproduced) were considered as references in analyses

affect the probability to lactate at 2 years of age (Jorgenson et al. 1993) and reproduction as a 2-year-old reduced body growth but had no obvious negative fitness consequences (Festa-Bianchet et al. 1995). The analyses we present here, based upon a much larger sample size and a wider range in ages of primiparity, produced three results with strong ecological and evolutionary implications. First, despite its major somatic cost, early maturity had no apparent negative fitness consequences. Second, delayed primiparity allowed small yearlings to attain similar adult mass as others ewes. Third, age of primiparity was heritable and directional selection favored earlier maturation.

As previously reported for ungulates (Jorgenson et al. 1993, Gaillard et al. 2000a) age of primiparity was strongly affected by environmental conditions during early development, as evidenced by the strong effects of both cohort and density as yearling. Our analyses, however, also revealed an interaction between population density and yearling mass on age at first reproduction, that became evident with the additional 15 years of data since Jorgenson et al. (1993). Ewes that were heavy as yearlings reproduced at a younger age than light yearling ewes only at low density. At high density, yearling females are on average smaller than at low density (Leblanc et al. 2001), and nearly all delayed primiparity independently of their mass. Population density as a yearling therefore had both direct and indirect impacts on age of primiparity. At low density, ewes that reached 50 kg as a yearling were typically primiparous at age two. At high density, however, 50-kg yearling ewes delayed first reproduction by two more years (Fig. 1). Light ewes were likely simply too small to reproduce, but density-dependent changes in age of primiparity for heavy ewes suggest a risk-averse reproductive strategy. Under harsh environmental conditions, young females postponed their first reproduction in favour of body growth, presumably to avoid compromising their future reproductive potential. Similarly to older ewes (Festa-Bianchet and Jorgenson 1998, Martin and Festa-Bianchet 2010), young bighorn ewes therefore appear to favor their own survival and body condition over any potentially risky allocation of resources to reproduction under harsh environmental conditions.

In addition to environmental conditions during early life, we revealed maternal effects on age of primiparity. Maternal effects influence lamb and yearling mass (Wilson et al. 2005) but also persist later in life, affecting age at first parturition. This result is important because it suggests that maternal

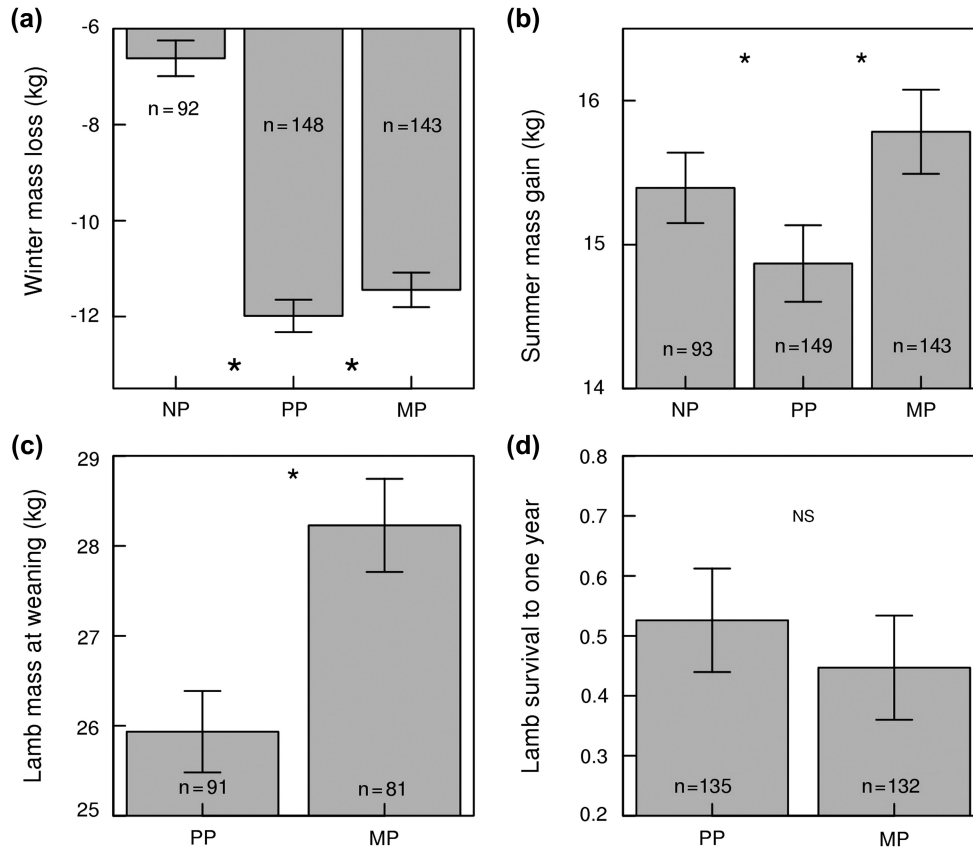


Figure 2. Means (and SE) of (a) winter mass loss, (b) summer mass gain, (c) lamb mass at weaning and (d) lamb survival to one year as a function of reproductive status for young (3–4 years old) bighorn ewes at Ram Mountain, Alberta. NP, PP and MP refer to nulliparous, primiparous, and multiparous females respectively. *Indicates a significant difference between two adjacent columns.

Table 3. Estimates of effects of lamb sex and maternal parity, age, mass before conception and density on mass on 15 September and survival to one year for bighorn lambs born to ewes aged 3 or 4 years at Ram Mountain, Alberta, from linear mixed models. Ewe identity and year were fitted as random effects. Parameters with a significant effect are in bold.

Fixed effects	Mass in mid-September (n = 169 lambs from 128 females over 30 years, R ² = 0.55)			
	Estimates	95% CI	p-value	
(intercept)	15.62	10.33	27.51	0.000
lamb sex [male]^a	1.93	0.63	3.13	0.003
parity[multiparous]^a	1.55	0.67	4.07	0.007
ewe age	-2.09	-4.72	-1.08	0.003
ewe mass before conception	0.29	0.14	0.42	< 0.001
density	-0.03	-0.06	0.01	0.096

Fixed effects	Survival to one year (n = 300 from 179 females over 33 years)			
	Estimates	SE	z	p-value
(intercept)	1.535	1.66	0.92	0.35
lamb sex [male] ^a	0.002	0.29	0.005	0.99
parity[multiparous] ^a	-0.41	0.42	-0.97	0.33
ewe age	0.15	0.31	0.50	0.61
ewe mass before conception	0.009	0.033	0.27	0.78
density	-0.023	0.009	-2.46	0.014

^a‘female lamb’ and ‘primiparous’ ewes were considered as references in analyses

care affects age at first reproduction of daughters. We previously reported that as population density increased, bighorn ewes reduced reproductive effort (Martin and Festa-Bianchet 2010). Our analysis suggests that the delay in age of primiparity with increasing density may not be entirely due to a direct effect of intraspecific competition. Instead, it could partly be induced by a decrease in maternal effort. These persistent maternal effects could have strong implications for populations dynamics, possibly inducing a lag in density-dependence (Ginzburg 1998, Benton et al. 2001) so that age of primiparity may not decline with decreasing density as quickly as it is delayed when density increases. That lag effect may partly explain why 2-year-old ewes had about a 50% lactation rate at a density of 30-35 ewes before the increase phase (Jorgenson et al. 1993), yet none of 20 2-year-old ewes lactated during the last 9 years of monitoring with less than 30 ewes.

In species that begin to reproduce before completing body growth, primiparity should decrease growth (Roff 2002). Our analyses revealed substantial tradeoffs between growth and primiparity. Primiparous females lost more mass during gestation than multiparous females. Their mass loss over winter was greater than that of nulliparous females of the same age, and they gained less mass during summer than either nulliparous or lactating multiparous females of the same age. Combining gestation and lactation, first reproduction led to a loss of 4 kg and 2.8 kg (8% and 6% of average mass) compared to nulliparous and multiparous ewes of the same age.

Table 4. Estimates of effects of age of primiparity and age on mass in September for bighorn females aged 1 to 6 years at Ram Mountain, Alberta, from a linear mixed model of 1034 mass measurements for 203 females from 1971 to 2008. The model explained 90% of the variance in body mass.

Fixed effects	Estimates	95% CI		p-value
(Intercept)	56.98	47.69	66.95	< 0.001
Age of primiparity (AP)	-9.44	-14.83	-4.68	< 0.001
AP²	0.74	0.13	1.41	0.016
Age	-0.56	-6.79	5.22	0.83
Age ²	0.53	-0.32	1.42	0.22
AP × Age	6.64	3.53	9.91	< 0.001
AP × Age²	-0.87	-1.32	-0.39	< 0.001
AP² × Age	-0.64	-1.05	-0.25	< 0.001
AP² × Age²	0.08	0.02	0.14	< 0.001
Random effects	Variance	% ^a	LRT ^b	p-value
Identity	11.99	0.47	433.94	< 0.001
Year	3.98	0.16	144.58	< 0.001
Residual	9.54			

^aproportion of variance; ^blikelihood ratio test

Small yearlings delayed primiparity and eventually attained a similar adult mass as ewes that were large as yearlings and started to reproduce at a younger age. Because we found no effect of yearling mass on survival to 6 years of age, we concluded that the decrease in mass difference with age was not due to differential mortality. To our knowledge, this is one of the first reports that a delay in primiparity allows for compensatory body growth in female mammals, overcoming early differences in mass due to environmental conditions or

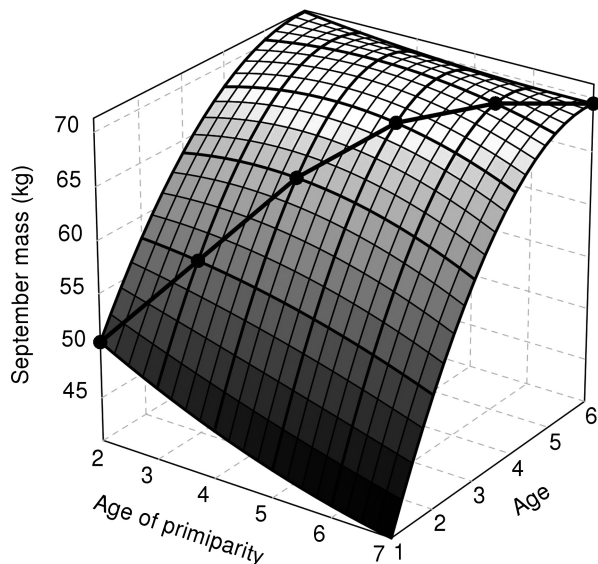


Figure 3. Prediction of mass in September for bighorn ewes aged 1–6 years at Ram Mountain, Alberta, as a function of age of primiparity and current age. The figure is based on the model reported in Table 4. Terms plotted in the figure explain 75% of variance in mass in September. Full circles and bold line indicate estimated mass in mid-September before first reproduction. A ewe primiparous at two years would have bred the previous November–December, when aged 18–19 months. The surface below the bold line shows the age-specific mass of females that have not yet reproduced.

maternal effects. In Columbian ground squirrel *Spermophilus columbianus*, nonreproductive 2-year-old females are smaller after emergence than reproductive ones, but gain more mass during summer (Broussard et al. 2008). Adult mass is important for survival and reproductive success (Gaillard et al. 2000b, Coltman et al. 2005). Thus, delaying primiparity is a conservative strategy for small individuals, favouring their own growth and future reproduction at the cost of current reproduction.

Before reproducing for the first time, a female should accumulate sufficient body resources to avoid comprising body growth and therefore adult mass. That is particularly important in view of our finding that the first reproduction involved greater somatic costs (greater mass loss in winter and lower mass gain in summer) than subsequent reproductive events. Because these estimates took into account the overall relationships between initial mass and mass change, they represent real somatic costs, rather than simply reflecting the fact that mass changes depend partly on individual ability to dispose of available resources (Pelletier et al. 2007).

Age of first parturition was influenced by additive genetic effects. Its heritability was low, as expected given the strong environmental variation. Heritability of age of primiparity in bighorn sheep was similar to that estimated for red deer (comparing models without maternal effects, Kruuk et al. 2000). Coltman et al. (2005) estimated a similar heritability but found it to be not significant. The use of a Bayesian method and a larger pedigree increased our power to detect additive genetic variation. The much higher heritability reported by Réale and Festa-Bianchet (2000; $h^2 = 0.53 \pm 0.33$) did not account for environmental and maternal variation in the estimation of additive genetic variance.

The survival to one year of lambs born to primiparous females was the same as that of lambs born to multiparous ewes of the same age, but primiparous females produced smaller lambs, suggesting either a reduced reproductive effort or inexperience. Lamb mass at weaning is an important fitness-related trait, because it is correlated with adult mass and reproductive success in females and with adult mass and horn length in males (Festa-Bianchet et al. 2000). Adult mass and horn length are the main determinants of reproductive success for rams (Coltman et al. 2002). Offspring of primiparous ewes are smaller and may have thus a lower reproductive success than lambs of multiparous ewes. Despite the strong somatic costs of first reproduction, however, its direct fitness consequences appeared limited. Longevity was independent of the age of primiparity, but lifetime reproductive success was reduced by late primiparity. Good environmental conditions could result in both early primiparity and greater lifetime reproductive success. The age of primiparity effect was significant despite the inclusion of population density and cohorts effects in the model, suggesting directional selection for earlier maturation in the Ram Mountain population. Females that started to reproduce earlier had higher reproductive success. Considering the heritability of age at primiparity we might expect a decrease in age at first parturition over time. Over the 33-year study, however, mean age of primiparity increased from 2.79 years (0.06 SE) in 1975–1985 to 3.38 (0.14 SE) in 1999–2009. That difference could not be explained by current population density because in the last 10 years density was

Table 5. Estimates of effects of age of primiparity, yearling mass and density as yearling on longevity and lifetime reproductive success (natural log+1) of bighorn ewes born from 1971 to 2000 at Ram Mountain, Alberta, from linear mixed models. Year of birth was fitted as random effects. Parameters with a significant effect are in bold.

Fixed effects	Estimates	95% CI	p-value	
Longevity (n = 187 over 29 years, $R^2 = 0.20$)				
(intercept)	2.47	-4.11	8.91	0.45
age of primiparity	-0.22	-0.92	0.48	0.53
yearling mass	0.12	0.0036	0.22	0.04
density as yearling	0.02	-0.01	0.06	0.17
Lifetime reproductive success (ln+1 transformed, n = 185 over 29 years, $R^2 = 0.38$)				
(intercept)	1.05	0.42	1.63	0.007
age of primiparity	-0.18	-0.24	-0.11	< 0.001
yearling mass	0.0028	-0.0081	0.012	0.58
density as yearling	-0.0042	-0.0072	-0.0012	0.014
longevity	0.12	0.11	0.14	< 0.001

lower than in 1975–1985. Other changes in environmental conditions, selection pressures on correlated traits or lag density-dependent effects (such as the maternal effects discussed above, or lags in vegetation growth) could induce this result.

We found important ecological and evolutionary implications of variability in age of primiparity for bighorn sheep. Late primiparity appears to result mostly from a conservative reproductive strategy rather than resource limitation. Delayed primiparity allows young females to compensate for low initial body mass and might increase their survival and reproductive success compared to a strategy of immediately investing scarce resources in reproduction. This reproductive strategy appears to favour maintenance over reproductive investment, similarly to the strategy of adult females in this population (Martin and Festa-Bianchet 2010).

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