Bighorn Ewes Transfer the Costs of Reproduction to Their Lambs

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ABSTRACT: Several studies of large mammals report no direct reproductive costs for females. Individual heterogeneity may hide fitness costs of reproduction, but mothers could also transfer some costs to their offspring. Using data on 442 lambs weaned by 146 bighorn sheep (*Ovis canadensis*) ewes at Ram Mountain, Alberta, we studied how reproductive effort varied with environmental and maternal conditions. During summer, lactating ewes should gain enough mass to survive the winter and to support their next gestation, while nursing their current lamb. We measured reproductive effort as summer mass gain by lambs corrected for maternal mass in June and maternal mass gain during summer. Females lowered their reproductive effort when population density increased and if they had weaned a lamb the previous year. A reduction in reproductive effort led to lower winter survival by lambs. Bighorn ewes have a conservative reproductive tactic and always favor their own body condition over that of their lambs. When resources are limited, ewes appear to transfer reproductive costs to their lambs, as expected from the much greater relative fitness consequences of a reduction in maternal than in offspring survival.

Keywords: bighorn sheep ewe, heritability, reproductive effort, life-history traits, parent-offspring conflict, fitness.

Introduction

Reproductive effort, the proportion of total energy budget that an organism devotes to reproduction (Williams 1966), is a fundamental concept of life-history theory (Stearns 1992). For iteroparous species, energy allocation to reproduction should depend on environmental variability and predictability (Hirshfield and Tinkle 1975). When resource availability is variable, rather than a fixed allocation to reproduction based on average conditions, natural selection should favor an adjustment of effort based on individual body condition and resource availability at each reproductive event (Clutton-Brock et al. 1996; McNamara and Houston 1996). Adjustment of energy allocation when

resource availability decreases could happen in three main ways (fig. 1). First, reproductive effort may remain unchanged, and both maternal and offspring conditions should decrease by the same order of magnitude (fig. 1A). Second, under a conservative tactic, energy allocation to reproduction could decrease, allowing mothers to maintain a stable condition but inducing a decrease in offspring condition (fig. 1B). Third, a risky tactic may involve an increase in reproductive effort, inducing a stable offspring condition but decreasing maternal condition (fig. 1C). Similarly, females confronted with an energetic cost of reproduction, such as that induced by an earlier reproductive episode, may adopt one of these three tactics to pay the cost. A conservative tactic may involve a transfer of the cost to the current offspring. Maternal condition would remain stable, while offspring condition would decrease. Thus, a female could reduce the fitness cost of reproduction by transferring her energy cost to her offspring. A transfer of costs would occur when the fitness costs of a female's reproduction are detectable only in her progeny. If females cannot predict yearly resource availability, they should adopt a conservative tactic to maximize their probability of survival (Hirshfield and Tinkle 1975). Environmental predictability should be particularly low when females conceive well in advance of the time of maximum effort (Hirshfield and Tinkle 1975), which in mammals is typically late gestation and lactation.

In temperate environments, most monotocous large mammals give birth and lactate in spring and summer, but juvenile survival is particularly constrained during winter (Sæther 1997; Gaillard et al. 2000b). Yearly variability in weather and population density makes these environments highly unpredictable for capital breeders such as ungulates (Stearns 1992) because females must conceive in late fall, yet the growth and survival of juveniles depend on resource availability several months later. Unpredictability should favor low reproductive effort to avoid compromising maternal survival because a female's fitness is more dependent on her survival than on her reproductive success in a given year (Gaillard and Yoccoz 2003). Over

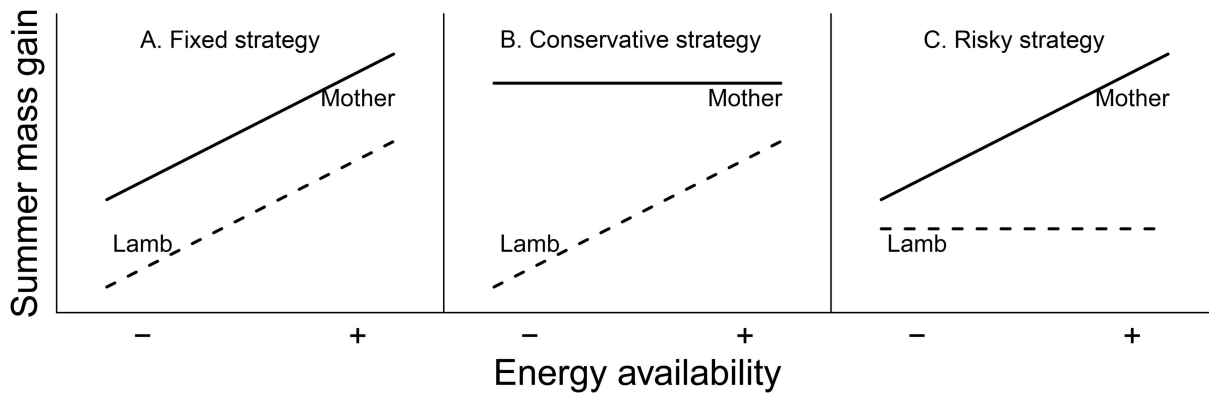* Corresponding author; e-mail: julien.martin2@usherbrooke.ca.

Figure 1: Variation of maternal and lamb summer gain as a function of energy availability expected under three reproductive tactics. *A*, Fixed: reproductive effort is constant, and both maternal and lamb condition vary. *B*, Conservative: a decrease in resource availability lowers reproductive effort. Maternal condition remains stable, but offspring condition decreases. *C*, Risky: because of increased reproductive effort, offspring condition remains stable as resource availability declines, but maternal condition declines.

a few months in summer, females must produce sufficient milk to wean an offspring, while building fat reserves for winter. Those reserves will affect both her survival and her next reproduction (Pelletier et al. 2007). Consequently, a trade-off between current and future reproduction should be manifest when comparing offspring growth and maternal mass accumulation during summer. Because very few field studies have documented mass changes and survival of mother-offspring pairs over several seasons, however, little is known about how mothers may allocate energy to themselves or their offspring (Festa-Bianchet and Jorgenson 1998; Crocker et al. 2001; Therrien et al. 2007; Bardsen et al. 2008).

Reproductive effort should vary according to environmental conditions (Hirshfield and Tinkle 1975), age (Roff 2002), predation risk (Candolin 1998), and body condition (McNamara and Houston 1996). Few studies, however, have considered how previous reproduction may affect current effort (sensu Hirshfield and Tinkle 1975; Johnson 1986). Life-history theory assumes that reproduction is costly (Stearns 1992; Roff 2002) for parents. Previous studies on large mammals, however, reported both existence (e.g., North American elk *Cervus elaphus* [Stewart et al. 2005] and moose *Alces alces* [Testa 2004]) and absence (e.g., bison *Bison bison* [Green and Rothstein 1991] and reindeer *Rangifer tarandus* [Weladji et al. 2008]) of direct fitness costs of reproduction for females. Females facing persistent energy costs of previous reproduction could transfer some of those costs to their current offspring by decreasing reproductive effort. The transfer of costs would favor both maternal survival and future reproduction. It would also decrease the fitness of the current offspring,

while reducing our ability to detect the direct fitness cost of reproduction for mothers.

Individual variation in reproductive potential limits the power of nonmanipulative studies to quantify trade-offs between life-history traits (Festa-Bianchet et al. 1998; Service 2000; Cam et al. 2002). Because of individual differences in reproductive potential, identity of the animal must be controlled for during statistical analysis, requiring a large data set (Festa-Bianchet et al. 1998). Here, we analyze a 30-year data set on individual reproductive success and seasonal mass changes of bighorn sheep to identify the factors influencing reproductive effort in an iteroparous and long-lived mammal facing a variable environment. We then quantify the influence of reproductive effort on both maternal and lamb survival.

Although several studies examined reproductive effort in mammals, there is no consensus on how to measure it (Hirshfield and Tinkle 1975; Stearns 1992). Reproductive effort should not be defined as a ratio, such as offspring over maternal mass at weaning, because ratios may not provide comparable estimates between age classes (Hirshfield and Tinkle 1975) and could lead to spurious correlations (Atchley et al. 1976). Furthermore, the use of ratios assumes an isometric relationship between the two traits, but both theory and empirical evidence have shown that most relationships between life-history traits are allometric (Roff 2002) and require fitting a regression (Atchley et al. 1976). Using offspring mass at weaning corrected for maternal mass in a linear regression framework would avoid these problems. Weaning mass in bighorn lambs, however, is strongly affected by parturition date (Feder et al. 2008). Bighorn ewes nurse their lambs until early autumn (Festa-

Bianchet 1988), and lamb mass-gain rate is independent of birth date (Feder et al. 2008). Before weaning, milk is the main source of nutrients for young mammals (Martin 1984; Lee 1996). Lactation is the most energetically costly component of female reproduction in many mammals (Martin 1984), and milk quantity is highly correlated with offspring mass gain (Robbins and Moen 1975; Garcia et al. 1999; Therrien et al. 2008). Therefore, we reasoned that the mass gain of offspring during lactation reflects the absolute amount of energy that a female devotes to reproduction. Consequently, lamb mass-gain rate could be a good metric of reproductive effort, when corrected for confounding variables. By definition, reproductive effort is the energy allocated in reproduction corrected for total maternal energy (Hirshfield and Tinkle 1975). Total maternal energy could be partitioned into reserves available before parturition and intake during lactation. Ewes that are heavy in early June gain less mass during summer than do light ewes (Pelletier et al. 2007), suggesting that mass in early June reflects body condition at the beginning of lactation. Maternal mass gain over summer should reflect energy intake. As a consequence, lamb mass gain, which represents energy allocated to reproduction, should be corrected for total maternal energy, separated into reserves (estimated by maternal mass in June) and intake (estimated as maternal summer mass gain; Hirshfield and Tinkle 1975). In addition, bighorn sheep are sexually dimorphic, and male lambs gain mass faster than do female lambs (Leblanc et al. 2001). To compare effort between reproductive events or between females, lamb sex should be taken into account in analyses of reproductive effort.

If maternal mass in June and summer mass gain reflect body condition at parturition and energy intake during summer, respectively, a ewe's mass gain should be negatively correlated with her mass in June and positively correlated with her lamb's summer mass gain. If ewes face a trade-off in allocating scarce resources to themselves or to their lamb, however, there should be a negative relationship between maternal and lamb mass gain. Lambs benefiting from high reproductive effort should have high survival. On the basis of earlier work (Festa-Bianchet and Jorgenson 1998), we expected ewes to decrease reproductive effort as density increased according to a conservative tactic (fig. 1*B*). We also examined the effects of other environmental variables that could affect the energy available to mothers, including an estimate of the quality of summer forage in the previous year and an index of environmental condition. In addition, we predicted that reproductive effort should decrease in the year after successful reproduction, defined as survival of the lamb to weaning. Furthermore, because sons are costlier than daughters (Bérubé et al. 1996), weaning a male should induce a greater de-

crease in reproductive effort the following year than does weaning a female.

Methods

Study Area and Population

Since 1971, bighorn sheep on Ram Mountain (52°8′N, 115°8′W; elevation 1,082–2,173 m), Alberta, Canada, have been captured several times each summer in a corral trap baited with salt (Jorgenson et al. 1993). Animals are marked using visual collars and plastic ear tags at their first capture (usually as lambs). 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 examined the udder to classify ewes as lactating or not lactating. During daily behavioral observations, ewes were classified as lactating if their lamb was alive. Yearly reproductive success of individual ewes was measured by lamb survival to September 15, which corresponds approximately to weaning (Festa-Bianchet 1988). Birth date was known for most lambs born since 1992 (Feder et al. 2008). Lamb-ewe matches were established through repeated observations of suckling.

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). Using repeated measurements of the same individual each summer, we adjusted body mass to spring (June 5) and fall (September 15) for each ewe. Spring mass of lambs was adjusted to June 15 because some were born after June 5 (Festa-Bianchet et al. 1996). We used linear mixed models with a restricted maximum likelihood method to adjust mass by fitting mass as a function of date (considering May 25 as day 1; Pelletier et al. 2007). We included random effects of individual identity as an intercept and the interaction between identity and date as a slope representing individual mass-gain rate. We fitted separate linear mixed models for each year and for each category (lambs and mothers) and used the predicted values of individual intercepts and slopes (provided by best linear unbiased predictions) to adjust individual mass. Summer mass gain was the difference between mass in September and that in June. Relative summer mass gain was defined as the gain corrected for mass in spring (Pelletier et al. 2007) and was calculated as the residuals of a regression model linking summer mass gain and mass in spring.

We measured yearly variability in the quality of summer forage using fecal crude protein (FCP; Blanchard et al. 2003; Feder et al. 2008). For fecal samples collected between May 31 and September 18 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).

We used the anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994) as an index of environmental conditions. Summers (June–August) with high NPI values tend to be warmer and dryer than summers with low NPI (mean temperature: $r = 0.30$, $P = .06$, $N = 34$ years; total precipitation: $r = -0.27$, $P = .12$, $N = 34$ years). These correlations were obtained with data from the Environment Canada weather station at Nordegg, about 20 km from Ram Mountain.

We used the number of adult females (≥ 2 years old) in June each year as an index of density (Festa-Bianchet and Jorgenson 1998). Following Pelletier et al. (2007), we considered two periods of contrasting environment, defined by population trajectory and lamb survival. The first period, before 1990, was characterized by an increasing population and high and stable lamb survival. After 1989, the population declined, and lamb survival was low and variable, after an apparent deterioration of environmental conditions.

Statistical Analyses

Because of strong variation in age of first reproduction (Jorgenson et al. 1993) and trade-offs between growth and early reproduction (Martin 2010), primiparous females were excluded from analyses to remove any bias associated with primiparity. Analyses of lamb summer mass gain were restricted to lambs that survived to September. Our analyses are based on 442 lamb-mother pairs with known summer mass gain, from 146 marked females, between 1977 and 2006. We used linear mixed models for all analyses, with mother identity and year as random effects. As no two-way interactions were significant, we removed them from our models (Engqvist 2005). All statistical analyses used R, version 2.8.0 (R Development Core Team 2008). Mixed models were fitted using the lmer function in lme4 (Bates et al. 2008), and fixed-effects probability and confidence intervals were assessed using pvals.fnc in languageR (Baayen 2009).

To evaluate which parameters affect maternal summer mass gain, we fitted a model of mass gain with mass in June, age, previous reproductive success (coded as "failed," "weaned a female," or "weaned a male"), lamb sex, study period, density, FCP the previous year, and summer NPI as fixed effects. To estimate parameters affecting reproductive effort, we fitted a model of lamb summer mass gain that included as fixed effects lamb sex, maternal mass gain, mass in June, age, previous reproductive success, study period, density, FCP, and summer NPI. Because we included mass in June in the fixed part of the model for maternal mass gain, all others parameters included in the

model can be interpreted as affecting a mother's summer mass gain relative to her initial (June) mass. Similarly, because the model of lamb mass gain included lamb sex, maternal summer mass gain, and maternal mass in June, all others parameters in this model can be interpreted as affecting reproductive effort. A recent review of population dynamics in large herbivores revealed that density typically has no negative effect up to a threshold, beyond which the negative effect of density is linear (Bonenfant et al. 2009). Density was thus fitted as a threshold effect. We used Akaike Information Criterion (AIC) to compare a model without a threshold (constant linear effect), one with no effect below the threshold and a linear effect above, and a model with linear effects both below and above a threshold, for different threshold values. The model with the lowest AIC was retained (Burnham and Anderson 2002).

We used a logistic regression framework to evaluate the effect of reproductive effort on lamb and maternal survival over winter. First, lamb survival was fitted as a function of reproductive effort, sex, maternal age, and study period. Maternal winter survival was assessed as a function of reproductive effort, lamb sex, maternal mass in September, maternal age, and study period. Maternal age was fitted as a threshold effect with a constant survival between 2 and 8 years and a declining survival after 8, as suggested by previous studies of the same population (Festa-Bianchet et al. 2003). Although maternal mass in June, summer mass gain, and age were correlated, collinearity was negligible in our models because all correlations were less than 0.5 (Glantz and Slinker 1990).

Results

Only age and mass in June affected summer mass gain of lactating ewes (table 1). Heavy females gained less mass than light ones, and young and old females gained relatively less mass than prime-aged ones (fig. 2). The effects of age and mass in June were similar in both study periods (age × period interaction: -0.27 ± 0.45 SE, $P = .50$; mass in June × period interaction: -0.07 ± 0.04 SE, $P = .08$). Density, summer weather, fecal crude protein, previous reproduction, lamb sex, and study period did not affect summer mass gain of lactating females (table 1). Summer mass gain of females was also independent of density, and no threshold effect improved the model (fig. 3; without a threshold, AIC = 1,967, and AIC > 1,972 for all models with a threshold density effect).

Lamb summer mass gain was greater for males than for females and increased with both the mother's summer mass gain and her June mass (table 2). Population density (fig. 3) and reproductive success of the mother the previous year had negative impacts on lamb mass gain (table

Table 1: Estimates of effects on summer mass gain of bighorn ewes at Ram Mountain, Alberta

	Estimate	95% confidence interval	P
Fixed effect:			
Intercept	13.91	−2.67, 24.43	
Mass in June	**−.18**	**−.17, −.09**	**<.001**
Lamb sex (male)	−.1	−.54, .25	.87
Previous reproductive success			.67
Weaned a female	−.2	−.55, .44	
Weaned a male	−.32	−.72, .34	
Age	**.84**	**.15, 1.03**	**<.001**
Age^2	**−.05**	**−.06, −.01**	**<.001**
Summer North Pacific Index	.57	−.10, 1.36	.54
Fecal crude protein	0	−.05, .05	.99
Density	−.02	−.05, .00	.36
Study period (after 1989)	.13	−.88, 1.60	.99

	Variance	Ratio	χ^2 (df)	P
Random effect:				
Female ID	.85	9.51	12.68 (1)	<.001
Year	5.02	56.04	221.26 (1)	<.001
Residual	3.08			

Note: Linear mixed model is based on 442 observations from 146 mothers over 30 years. Significant effects are in bold. Female lamb, not lactating, and first period of the study (before 1990) were considered as references in the lamb sex, previous reproductive success, and study period analyses, respectively.

2). A model with no effect of density below 65 individuals and a linear effect above best fitted the data on lamb mass gain (AIC = 1,876; fig. 3), although thresholds between 50 and 70 had similar AIC values. Models without a threshold and models with a linear effect below and above the threshold had higher AICs (>1,880). The effect of density was negligible when there were fewer than 65 adult females but was substantial as the population increased further. Lamb mass gain decreased by 2.7 kg (about 14%) as the population increased from 65 to 103 ewes (table 2; fig. 3). Lambs born to ewes that had weaned a daughter or a son the previous year gained, respectively, 0.68 and 1.27 kg less than lambs whose mothers failed to wean the previous year. Study period affected lamb mass gain (table 2), but the effects of maternal mass in June and maternal mass gain were independent of period (maternal mass in June × period interaction: −0.12 ± 0.07 SE, P = .12; maternal mass gain × period interaction: −0.02 ± 0.03 SE, P = .76). Lambs born after 1989 gained 1.5 kg less than lambs born before 1990. A nearly significant quadratic effect of maternal age suggested a decrease in mass gain for lambs born to very old mothers (table 2). Summer weather and FCP did not affect lamb summer mass gain (table 2).

Maternal identity led to significant individual variation in mass gain for both mothers and their lambs (ID random effects in tables 1, 2), and there was significant variability

among years in both analyses. No environment-by-individual interactions were significant (P values > 0.1; analyses not shown), suggesting that all individuals responded similarly to environmental changes.

Lamb winter survival increased with maternal reproductive effort (0.14 ± 0.06, z = 2.429, P = .015), sons had lower winter survival than daughters (−0.68 ± 0.25, z = −2.77, P = .005), and lambs born after 1989 had lower survival than those born earlier (−1.81 ± 0.34, z = −5.26, P < .001). Maternal winter survival increased with mass in September (0.11 ± 0.02, z = 4.33, P < .001) and with reproductive effort (0.11 ± 0.06, z = 1.98, P = .047). Survival decreased with age, for females older than 8 years (−0.34 ± 0.07, z = −4.69, P < .001).

Discussion

Our analysis led to four important results: (1) summer mass gain of lactating females was independent of environmental and reproductive variables, (2) lamb summer mass gain was substantially reduced by previous reproduction of the mother and by population density, (3) reproductive effort affected lamb survival, and (4) females showed consistent individual variation in reproductive effort. The smaller relative mass gain of young and old lactating females suggests a higher reproductive cost than for prime-age ewes. As females reached prime age, the costs
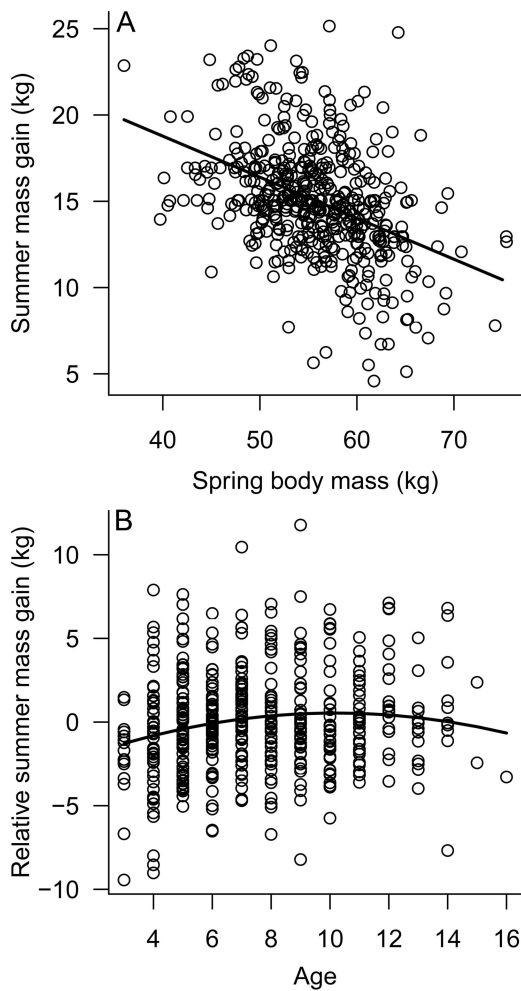
reach their individual-specific mass in late summer. Given a fixed amount of resources acquired over the summer, a female in good condition in June could allocate fewer to herself and still reach sufficient mass to survive and reproduce successfully the following year. Females that are heavy in June can then allocate more resources to maternal care. The positive correlation between maternal and lamb summer mass gain with no interaction with resource availability suggests that more energy was allocated to lambs only when maternal energy intake was high. Some females appeared able to ensure high mass gain for their lambs without increasing reproductive effort (Hirshfield and Tinkle 1975).

Summer mass gain by lactating females was not affected by either previous reproduction or environmental variability. Both variables, however, had a strong impact on
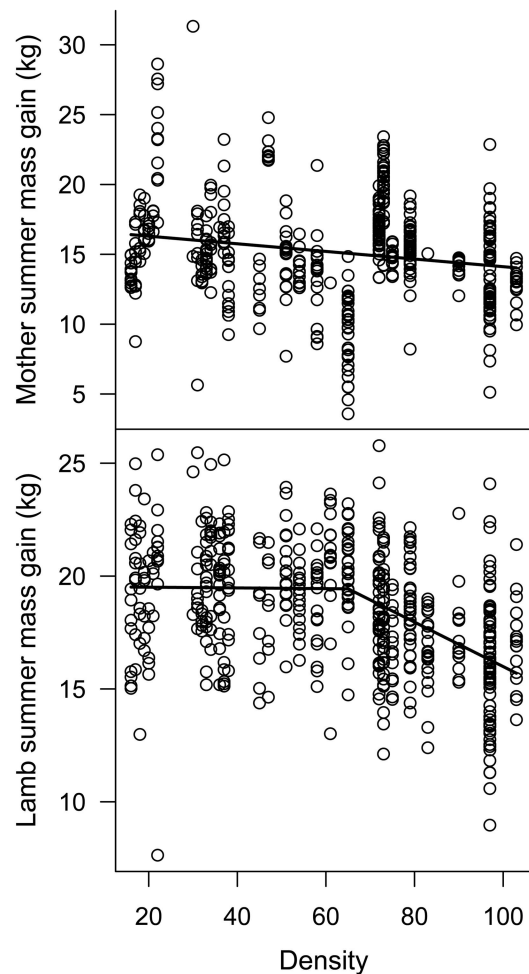

Figure 2: Effects of body mass (adjusted to June 5) and age on summer mass of lactating bighorn ewes at Ram Mountain, Alberta. *A*, Effect of June 5 mass on summer mass gain; *B*, variation of relative summer mass gain (summer mass gain corrected for June mass) with age.

of reproduction were likely lowered by the completion of body growth and increased maternal experience (Weladji et al. 2006). Senescence (Bérubé et al. 1999) likely lowered mass gain for older females. Because lactating females that were lighter in spring gained more mass during summer, we considered that age-adjusted mass in early June reflects female body condition at parturition, which is mostly from May 20 to June 5 (Feder et al. 2008). Summer mass gain of lactating ewes appeared independent of the environmental effects we measured. Individual adult females are highly consistent in the mass they reach by mid-September (Festa-Bianchet et al. 1996; Pelletier et al. 2007). Because small differences in September mass compared to an individual ewe's multiyear average affect her reproductive success (Festa-Bianchet 1998), it is important for ewes to

Figure 3: Variation of summer mass gain for bighorn sheep mothers (*top*) and lambs (*bottom*) according to population density on Ram Mountain, Alberta. Lines indicate model fitted to the data.

Table 2: Estimates of effects on the summer mass gain of bighorn lambs and the reproductive effort of their mothers at Ram Mountain, Alberta

	Estimate	95% confidence interval	P
Fixed effect:			
Intercept	13.28	4.00, 20.94	
Maternal summer mass gain	**.11**	**.04, .20**	**.003**
Maternal mass in June	**.11**	**.07, .16**	**<.001**
Lamb sex (male)	**1.65**	**1.27, 1.98**	**<.001**
Previous reproductive success:[a]			
Weaned a female	**−.68**	**−1.09, −.20**	**.005**
Weaned a male	**−1.30**	**−1.76, −.80**	**<.001**
Maternal age[a]	.30	−.14, .63	.188
Maternal age^2 [a]	−.02	−.04, 3.9E − 3	.068
Summer North Pacific Index[a]	−.05	−.47, .41	.894
Fecal crude protein[a]	−.01	−.04, .01	.369
Density (>65)[a]	**−7.23E − 2**	**−.11, −.04**	**<.001**
Study period (after 1989)[a]	**−1.20**	**−2.15, −.42**	**.005**

	Variance	Ratio	χ^2 (df)	P
Random effect:				
Mother ID	.87	20.35	33.89 (1)	<.001
Year	.76	22.42	57.10 (1)	<.001
Residual	2.63			

Note: Linear mixed model is based on 442 lambs born to 146 ewes over 30 years. Significant effects are in bold. Density was fitted as a threshold with no effect below 65 and a linear effect above. Female lamb, not lactating, and first period of the study (before 1990) were considered as references in the lamb sex, previous reproductive success, and study period analyses, respectively.

[a] Because reproductive effort was measured as lamb summer mass gain corrected for lamb sex, maternal mass in June, and maternal mass gain over the summer, these are effects on reproductive effort.

lamb mass gain. The relationship between reproductive effort and density became evident only after the population increased beyond about 65 adult females. Lamb mass gain might be influenced by direct density effects on forage availability or by density-related increases in parasite load. Both factors, however, should also decrease maternal mass gain and would not be expected to vary with maternal mass or maternal reproductive effort. Mass at weaning is an important fitness-related trait. In addition to having a direct effect on lamb survival, it is positively correlated with adult mass for both sexes, with lifetime reproductive success for females, and with horn size for rams (Festa-Bianchet et al. 2000). Our analyses suggest that when environmental conditions deteriorated, bighorn ewes reduced their reproductive effort. They raised smaller lambs with low reproductive potential and favored instead their own survival and future reproduction. Lambs bore the consequences not only of environmental variability but also of their mother's reproductive status the previous year. Successful reproduction the previous year did not affect the summer mass gain of ewes but decreased that of their lambs. Ewes that weaned a lamb lowered their reproductive effort the following year, particularly if they had

weaned a male, confirming the higher reproductive cost of sons (Bérubé et al. 1996).

The conservative reproductive tactic of bighorn ewes involves decreasing reproductive effort to compensate for environmental variation and previous reproductive costs. Lambs pay part of their mother's reproductive costs because ewes first ensure their own summer mass gain and allocate only surplus energy to their young (Festa-Bianchet et al. 1998). Because a conservative reproductive tactic would hide direct reproductive cost on female traits, studies of the costs of reproduction should consider both the direct effects of reproductive effort on female traits and its indirect effects on offspring traits. For long-lived iteroparous species in variable environments, fitness components whose variation has the greatest impact on the population growth rate, such as adult female survival, should have low temporal variability, a phenomenon referred to as environmental canalization (Gaillard and Yoccoz 2003). Females could lower the fitness costs of reproduction by decreasing reproductive effort when resources are scarce, to survive and reproduce in better years (Murphy 1968; Roff 2002). That tactic would decrease survival variability despite environmental stochasticity, leading to

adaptive canalization of adult female survival against environmental variability (Gaillard and Yoccoz 2003). From a population-dynamics perspective, a conservative maternal tactic could reduce recruitment during prolonged periods of poor or deteriorating environmental conditions beyond what may be predicted on the basis of resource availability alone (Proaktor et al. 2008). For the current offspring, a conservative maternal tactic constrains energy intake and should increase mother-offspring conflict. To compensate for limited maternal care, lambs could increase the frequency of suckling attempts and spend more time foraging on vegetation, as reported for white-tailed deer (*Odocoileus virginianus*) fawns whose mothers were subjected to an experimental reduction in food availability (Therrien et al. 2008).

Because we did not manipulate reproductive effort of our study animals, our research is based on correlative evidence, which has been criticized for not accounting for individual differences in reproductive potential (Reznick 1985; van Noordwijk and de Jong 1986). If those differences were ignored, the decrease in lamb (but not ewe) mass gain and survival with decreased resource availability could be interpreted as simply due to lambs being less able than adults to cope with environmental variability. Mothers could simply be unable to provide sufficient care to lambs at high population density or after years of successful reproduction. Our study, however, partially accounted for individual differences by including maternal mass and mass changes, two characteristics that affect reproductive potential (Gaillard et al. 2000*a*; Pelletier et al. 2007). Where feasible, manipulative studies of reproductive effort are desirable and have been performed in the wild (Moreno et al. 1997). Manipulations of mammalian reproductive effort are difficult (Neuhaus 2000) because of highly developed mother-offspring recognition mechanisms. By closely monitoring mass changes and survival of mother-offspring pairs over several years, we were able to establish that lamb mass gain and survival were affected by a maternal allocation strategy.

We conclude that the conservative reproductive tactic of bighorn ewes shifts most fitness costs of previous reproduction on their current lamb. Lambs are sensitive to population density, while ewes appear able to ensure their own maintenance independently of changes in resource availability. Accordingly, a review of ungulate population dynamics suggests that prime-aged females show little sensitivity to the environmental variables that affect juvenile survival, including weather, population density, and, in some cases, predation (Gaillard et al. 2000*b*). Previous studies sought to detect direct reproductive costs on maternal traits. For species with a conservative reproductive tactic, however, indirect costs that are shifted to offspring can be very important.

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Bighorn ewe with lamb in June at Ram Mountain, Alberta, Canada. Photograph by Julien G. A. Martin.