Despite Catch-Up, Prolonged Growth Has Detrimental Fitness Consequences in a Long-Lived Vertebrate

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ABSTRACT: Individuals experiencing poor growth early in life may later make up their size deficit. Compensatory growth or growth prolongation may lead to such catch-up, involving different life-history trade-offs under natural conditions. Frequent recaptures and detailed monitoring of animals surviving to asymptotic size are required to compare growth tactics and their fitness consequences. No study to date has obtained such detailed information for wild animals. We used repeated mass measurements (mean 11.6/animal) spanning the lifetime of 104 bighorn ewes (*Ovis canadensis*) to quantify growth tactics and identify the determinants and life-history costs of these tactics. Growth prolongation, not compensatory growth, led to partial catch-up: mass difference at age 7 was reduced to 4%, for two groups that differed by nearly 20% as yearlings. Ewes that had been light as yearlings prolonged their growth regardless of density or age of primiparity. Growth prolongation did not affect fecundity or longevity. Ewes that experienced poor early growth prolonged growth at the expense of reproductive fitness, weaning a smaller proportion of their lambs. By tracking multiyear growth patterns and comparing events at different life-history stages, we quantified a trade-off between growth and reproduction that would be overlooked if only the adult phenotype was considered. Compensatory growth in long-lived animals appears unlikely when early growth restrictions are mostly density dependent.

Keywords: bighorn sheep, compensatory growth, growth tactics, life-history traits, reproductive success.

Introduction

The idea that animals that experience unfavorable conditions early in life "make the best of a bad job" is widely accepted (Dmitriew 2011) and shapes our understanding of life-history theories; however, there are few empirical data on wild vertebrates to assess what "the best" might be. In fluctuating environments, changes in resource abundance, climate, or population density affect early development

(Metcalfe and Monaghan 2001). Often, poor early-life conditions increase mortality (Clutton-Brock et al. 1985; Thessing and Ekman 1994; De Kogel 1997). For individuals that survive the period of resource shortage, catch-up growth may mitigate the effects of a bad start. This plastic response, however, might incur long-term costs, especially if it forced a trade-off with other fitness components. Adaptations to cope with periods of growth restriction are important in fluctuating environments, because in many species adult size is a strong determinant of fitness (Peters 1983; Choudhury et al. 1996; Ellers et al. 1998; Gaillard et al. 2000). Low resource availability during early development may limit growth (Blanckenhorn 1999; Konarzewski et al. 1996; Hewison et al. 2002), increasing early mortality and delaying first reproduction (Festa-Bianchet et al. 1997; Martin and Festa-Bianchet 2012). Tactics to counter an initial growth deficit have been documented in most vertebrate taxa (Wilson and Osbourn 1960; Hector and Nakagawa 2012). Wild animals can at times recover either partially or completely from early growth reductions (Green and Rothstein 1991; Bjorndal et al. 2003; Bize et al. 2006). Alternative growth tactics in response to poor initial growth, however, may entail fitness costs by lowering resource allocation to other life-history traits (Mangel and Munch 2005). These fitness costs have been documented in laboratory studies (Auer et al. 2010; Dmitriev 2011; Lee et al. 2012), but we know of no equivalent studies in the wild, where many ecological and environmental variables may affect resource allocation. For example, increased foraging time (Watkins et al. 1991) may entail a higher risk of predation or exposure to parasites. Strong cohort effects in body mass in some wild vertebrates (Pettorelli et al. 2002) suggest that catch-up growth does not always occur. Compensatory growth requires high resource availability, which may not be the case if unfavorable conditions caused by high density persist over several years.

Growth tactics are distinct patterns of changes in growth rate relative to other individuals of the same age. Jobling

(2010) defined catch-up growth as any instance when the growth trajectories of animals with different growth histories converge. After a period of growth restriction, individuals will be smaller than those that grew under better conditions but may later catch up. The term "catch-up growth" does not specify how the initial size difference is reduced. Compensatory growth occurs when, following growth restriction, animals grow more rapidly than size-matched conspecifics that did not encounter growth restrictions. This definition takes into consideration the effects of size on absolute growth rate: larger animals can achieve a given absolute growth rate through lower relative growth rates than smaller animals, attaining the same mass gain with lower metabolic cost or growth effort. Compensatory growth, however, is not necessary to achieve catch-up (Metcalfe and Monaghan 2001; Jobling 2010). Growth of many animals decreases or stops at sexual maturity (Bize et al. 2006; Charnov 2008; Nussey et al. 2011), and catch-up could simply involve growth prolongation after others cease growing. Compensatory growth and growth prolongation are not exclusive. Here, we refer to different growth tactics using terminology proposed by Jobling (2010) and the term "growth prolongation."

Different growth tactics may lead to different costs. Compensatory growth involves abnormally high growth rates, which can require more time spent feeding and increased exposure to predators (Gotthard 2000). Costs of compensatory growth at the cellular level may manifest themselves later in life (Metcalfe and Monaghan 2001) and decrease longevity (Jennings et al. 1999; Dmitriew and Rowe 2007) or reproduction (Auer et al. 2010; Lee et al. 2012). Growth prolongation requires higher growth rate than that of conspecifics of similar age that have stopped or reduced growth and may involve fitness costs similar to those of compensatory growth. Compensatory growth, however, usually occurs before sexual maturation (Sorci et al. 1996; Jennings et al. 1999; Gotthard 2000), while growth prolongation often delays maturation (Green and Rothstein 1991; Alonso-Alvarez et al. 2006), with two important implications: growth prolongation may occur at the expense of reproduction, and some costs of prolongation could be offset by avoiding the costs of reproduction (Beckman and Ames 1998). Therefore, the principal long-term cost of growth prolongation should be lower lifetime reproductive fitness because of delayed primiparity.

Adult mass is an important determinant of fitness in large mammals because it influences reproduction (Hewison and Gaillard 2001) and longevity (Bérubé et al. 1999; Gaillard et al. 2000). Despite substantial heritability (Coltman et al. 2005), adult mass can be negatively affected by restrictions on growth during early development (Pettorelli et al. 2002) from environmental (Festa-Bianchet et al. 2000) or maternal effects (Landete-Castillejos et al.

2009). Although several studies reported catch-up growth in wild large mammals (Green and Rothstein 1991; Rughetti and Festa-Bianchet 2010; Martin and Festa-Bianchet 2012), we know little about the underlying tactics and possible costs of catch-up growth, partly because no study obtained the frequent recaptures required to distinguish between compensatory growth and growth prolongation. An assessment of growth costs requires a comparison of individual growth patterns with lifetime reproduction and longevity. Studies on humans have shown multiple later-life effects of poor initial growth (von Borsdoff et al. 2011). No study of wild mammals, however, has documented the lifetime growth, survival, and reproduction of enough individuals to undertake such analyses. Here we analyze 37 years of data on individual mass changes during ontogeny, reproductive success, and longevity of female bighorn sheep (*Ovis canadensis*) to determine whether compensatory growth or growth prolongation contributes to catch-up growth and what are the long-term costs of different growth tactics for iteroparous and long-lived mammals in a variable environment. More specifically, we sought to test whether the fitness costs of catch-up among ewes that survived to adulthood could explain differences in three proxies of reproductive fitness (lifetime fertility, weaning success, and reproductive success) that cannot be accounted for by differences in adult mass. Our study offers a rare opportunity to examine whether differences in how animals achieve a given adult mass may affect the fitness consequences of that mass.

Bighorn sheep gain mass until 5–8 years old, but yearly net mass gains decrease at each age past 2 years (Nussey et al. 2011). Mass gain during summer is followed by mass loss in winter (Festa-Bianchet et al. 1996; Pelletier et al. 2007), while senescence-associated mass loss begins at about 11 years of age (Bérubé et al. 1999). In bighorn ewes, mass is associated with earlier primiparity (Jorgenson et al. 1993; Martin and Festa-Bianchet 2012), reduced reproductive costs (Festa-Bianchet et al. 1998) and earlier parturition date (Feder et al. 2008). Mass also increases longevity (Bérubé et al. 1999; Gaillard et al. 2000). High population density decreases lamb mass gain because ewes reduce maternal care when resources are scarce (Festa-Bianchet and Jorgenson 1998; Martin and Festa-Bianchet 2010), leading to a negative correlation between density and yearling mass (Leblanc et al. 2001). Given the importance of mass for fitness-related traits, a catch-up growth tactic should be expected following poor early development. Indeed, light yearling ewes that delay reproduction reach similar adult mass as heavy yearlings that enjoy earlier primiparity (Martin and Festa-Bianchet 2012). The growth strategy used by ewes following growth restriction during early development, or any fitness consequences of that strategy, remain unknown. We predicted

that ewes should demonstrate growth prolongation rather than compensatory growth. We also expected that growth prolongation should be prevalent at high density, when ewes are smaller as yearlings (Leblanc et al. 2001).

Methods

Study Area and Population

Bighorn sheep have been studied on Ram Mountain (52°N, 115°W; elevation 1,082–2,173 m), Alberta, Canada, since 1971. Repeated surveys and captures are carried out from late May to late September or early October. Data used here were collected from 1974 to 2011. Sheep are caught in a corral trap baited with salt. At their first capture, usually as lambs, they are assigned an identity number and marked with ear tags for future identification. Since 1974, more than 95% of the population has been marked (Jorgenson et al. 1993). Most adult females are caught 2 to 5 times per season. At each capture, the mass of ewes in kilograms (kg) is recorded and their udder is checked for lactation. Ewes with colostrum are considered pregnant. Most are later seen with a lamb or show an obvious loss of mass at a subsequent capture. Lamb-ewe associations are determined though observations of suckling. Since 1988, maternal links have been confirmed by microsatellites analyses (Poissant et al. 2008). More details of our capture and marking protocol are provided in Festa-Bianchet et al. (1996).

As in previous studies, we measured population density as the number of adult ewes in June (Festa-Bianchet and Jorgenson 1998; Leblanc et al. 2001). The population increased from 1980 to 1992, then declined until about 2004, and then increased slightly (Rioux-Paquette et al. 2011). We used the number of adult ewes in the year of birth as an index of density during early development. The age of primiparity is the age of first parturition, 6 months after first conception. Each year, females with milk or colostrum at first capture were considered to have produced a lamb. We calculated fecundity as the number of lambs produced by a ewe over her lifetime. Lambs were considered weaned if they survived to September 15. We calculated lifetime weaning success as the proportion of lambs produced by a ewe that were weaned and lifetime reproductive success as the total number of lambs weaned. Ewe longevity was the age at which a ewe was last observed. Resighting rate for ewes was over 99% (Jorgenson et al. 1997), and ewes that disappeared were considered dead.

Within-Season Mass Adjustment

The complete data set included 7,129 mass measurements of 515 females from 1974 to 2011, aged from a few days to 19 years. Mass measurements of pregnant females (usu-

ally obtained in late May or early June) were excluded. Ewe mass fluctuates seasonally by as much as 30% (Festa-Bianchet et al. 1996; Pelletier et al. 2007), increasing during late spring and summer then decreasing in winter. Consequently, almost all sheep are lighter at their first capture in one year than at their last capture the previous year. Thus, to model individual interannual growth, we controlled for seasonal variation for all age classes except lambs. We adjusted mass of sheep aged 1 year and older to September 15, the approximate peak summer mass of adult ewes (Festa-Bianchet et al. 1996; Pelletier et al. 2007).

Lambs. We used all available mass measurements of lambs to model growth. Lamb mass increases over the summer (Festa-Bianchet et al. 1996). The next mass included in growth models was on September 15 as a yearling.

Yearlings. Following Festa-Bianchet et al. (1996), we used individual linear regression of mass on date to adjust mass to September 15. We used yearling mass adjusted to September 15 as an indicator of early growth. Yearling mass is the last prereproductive estimated mass for ewes that reproduced at age 2.

Adults. For sheep 2 years old and older, we adjusted mass as described by Martin and Pelletier (2011). We used linear mixed models (LMM) with restricted maximum likelihood (REML) with mass as a function of the square root of capture date, taking May 25 as day 1. We included sheep identity and the interaction between identity and date of capture as random effects. We fitted a separate model for each year to estimate initial mass (intercept) and growth rate (slope) for each individual, then adjusted individual mass to September 15, using the lmer function of the lme4 library in R (R Development Core Team 2010). We defined adult mass as mass adjusted to September 15 at age 7 (Festa-Bianchet et al. 1996). Therefore, our analysis was limited to ewes that survived to at least 7 years of age.

Growth Curve Modeling

We modeled interannual growth of individual sheep using the Lopez equation (Lopez et al. 2000), a generalized Michaelis-Menten equation (Michaelis and Menten 1913) in which W is mass at age t, W_0 and W_f are the values of W at initial and infinite time, and K and c are constants:

$$W = \frac{W_0 K^c + W_f t^c}{K^c + t^c}.$$

The Lopez equation adequately describes mass gain patterns of ungulates (Lopez et al. 2000), including bighorn

sheep ewes (fig. 1). We chose it over other standard growth functions such as Weibull, Gompertz, or Richards because it is capable of describing sigmoid and diminishing returns growth and has more biologically interpretable parameters: W_0 (mass at time 0), W_f (asymptotic mass) and K (time when half of W_f is reached). Its flexibility permits a better adjustment to individual growth patterns, which may exhibit either diminishing returns or weakly sigmoid behavior.

Because senescence-associated mass loss begins at 11 years of age (Bérubé et al. 1999) and the Lopez equation cannot account for mass loss, we restricted modeling of mass to ages 0 through 10. A minimum of five data points are necessary to estimate the four-parameter Lopez function. To estimate reliable values of initial mass (W_0) and infinite-time mass (W_f), we required at least one mass measurement as a lamb and one between the ages of 7 and 10. We expected that most variation in growth tactics would occur in association with the timing of first reproduction. More than 95% of ewes that reproduced were primiparous between the ages of 2 and 5. Hence, we limited analyses to females with at least four data points between ages 0 and 5. These criteria restricted our sample to 112 ewes, with an average of 11.6 mass measurements each (range 6–20).

We performed nonlinear regressions using least-square estimates to fit individual growth curves of sheep mass in kilograms as a function of age in days, with day 0 being May 24 of the birth year (Feder et al. 2008). We used the nls package of the nlme library in R (R Development Core Team 2010), which returned estimates for each of the four parameters of the Lopez equation. To avoid unrealistic estimates of initial mass and asymptotic mass, we constrained the model to estimate W_0 values of 5 kg or less and W_f values of 90 kg or less. These constraints are conservative since bighorn lambs are rarely heavier than 5 kg at birth (Hass 1995) and the heaviest mass estimate for a ewe on September 15 was 89 kg. The curve fitting procedure did not converge for seven ewes that were excluded from analyses. We also excluded one ewe whose estimates revealed obvious measurement errors, reducing the sample to 104. The Lopez equation provided a good fit for 93% of females.

We needed individual estimates of growth duration to determine whether growth prolongation occurred in our sample. The growth rate (dW/dt) of the Lopez equation never decreases to zero; therefore, we needed to select a threshold to identify the end of growth. We defined growth duration as the time when individual growth rate reaches 2.5% of current body mass per year, based on year-to-year changes in mass of ewes that appeared to have completed their growth, according to the analysis by Nussey et al. (2011). This relative measure accounts for differences in
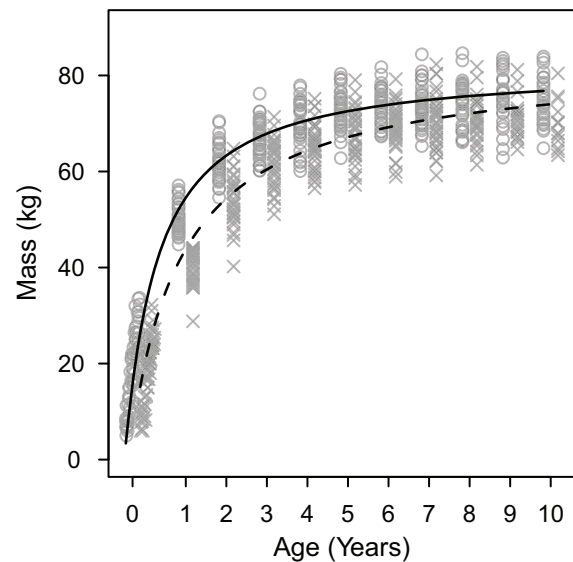
Figure 1: Age-specific mass and estimated average growth curves for bighorn sheep ewes that were heavy (circles, solid line) and light (x shapes, dashed line) as yearlings on Ram Mountain, Alberta. Ewes that as yearlings weighed more than the median mass (44.1 kg) were considered heavy. Ewes that weighed as much or less than the median mass were considered light. Lamb mass was measured at capture, and all other masses are adjusted to September 15 at each age. Only ewes whose growth was modeled are included.

adult mass by considering relative growth rate. We solved the derived Lopez equation (Lopez et al. 2000)

$$\left| \frac{dW}{dt} = \frac{ct^{c-1}(W_f - W)}{K^c + t^c} \right|$$

numerically for $dW/dt = 0.025/365\ W$ to obtain growth duration for each ewe in our sample.

Statistical Analyses

We first determined whether compensatory growth or growth prolongation were consistent with the growth patterns of ewes. To assess if growth prolongation occurred, we fitted a linear model of growth duration with yearling mass as fixed effect. To test for compensatory growth, we examined the relationship between the age at which a certain mass was reached and the growth rate at that mass. Ewes encountering growth restrictions will reach a given mass at a later age. If they experienced compensatory growth they would then show higher growth rates later in life, leading to a positive relationship between the age when a given mass is reached and growth rate at that mass. We solved the Lopez equation for age (t):

$$t = \left(\frac{W_0 K^c - W K^c}{W - W_f}\right)^{|1/c|}.$$

We calculated t for mass (W) values of 40, 50, and 60 kg for all ewes, using their individual growth curve parameters. These masses are typical for ewes aged 2–7 years (fig. 1), when compensatory growth might occur. We then used the derived Lopez equation to calculate individual growth rates (dW/dt) for each W according to the age (t) when it was reached (fig. 1B). For each mass, we fitted a linear model of growth rate as a function of age when the mass was attained. Age at mass and growth rate data were log transformed to linearize the relationship.

Because we found no evidence of compensatory growth, we focused subsequent analyses on growth prolongation. We fitted an LMM of growth duration with yearling mass, population density and age of primiparity as fixed effects. To assess whether growth duration affected longevity, we fitted an LMM of longevity and growth duration, yearling mass, adult mass, and population density as fixed effects. Finally, to identify which components of reproductive fitness were affected by growth duration, we fitted GLMMs of lifetime fecundity with a Poisson distribution and of lifetime weaning success with a binomial distribution. To evaluate the effect of growth duration on lifetime reproductive success, we fitted a GLMM of reproductive success with a Poisson distribution and growth duration, age of primiparity, and adult mass as fixed effects. In all models, fixed effects were growth duration, age of primiparity, population density, yearling mass, longevity, and adult mass.

We fitted mixed effects models with restricted maximum likelihood, beginning with maximal models that included all fixed variables described above and maternal identity or year of birth as random variables. We compared each mixed model to an equivalent model without random effect with likelihood ratio tests to assess the significance of the random variables (Zuur et al. 2009). Significant random variables were kept in subsequent models; otherwise analyses proceeded without random effects. We then used backward selection for models estimated with maximum likelihood (Zuur et al. 2009), successively deleting the least significant variable until all remaining variables were significant ($\alpha = 0.05$). To ensure that the removal of variables did not significantly reduce model fit, we performed likelihood ratio tests or ANOVAs of model residual deviance at each step of model selection. In each model, we calculated variance inflation factors (VIFs) of variables, which measures multicollinearity of covariates in a model (Zuur et al. 2010).We used a VIF threshold of 3 (Zuur et al. 2010), above which multicollinearity was considered problematic. Two-way interactions caused multicollinearity and

were not significant (all $P > .05$), so we omitted them from analyses.

All modelling was done in R (R Development Core Team 2010). Linear models and linear mixed models were fitted using the gls and lme functions of the nlme library (Pinheiro et al. 2012). Generalized linear and mixed models were fitted using the glm and glmer functions of the lme4 library (Bates and Maechler 2010), respectively. Data used for this article are in the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.36951 (Marcil-Ferland et al. 2013).

Results

Growth duration averaged 5.70 ± 0.18 years (range 3.55–8.50) and decreased linearly with yearling mass ($\beta = -0.107 \pm 0.027$, $P > .001$; fig. 2). Growth duration was associated ($\beta = 1.75 \pm 1.12$, $P = .003$) with increased mass gain between ages 1 and 4. The average difference between yearling ewes lighter and heavier than the median mass was 9.7 kg (19.4%). The difference in mass between these two groups of ewes decreased to 3.2 kg (4.3%) by age 7 (fig. 1). Ewes that had poor growth early in life maintained lower mass-specific growth rates, as the age at which ewes attained a certain mass reduced their growth rate at that mass (table 1).

In a model that considered yearling mass as well as environmental and reproductive parameters, yearling mass was the only fixed effect that affected growth duration
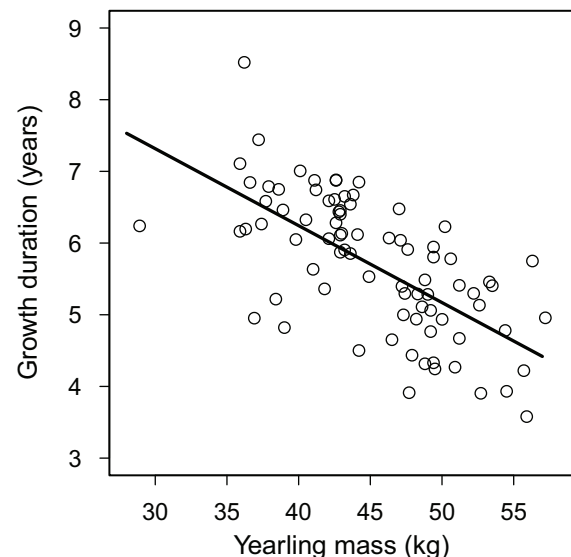
Figure 2: Effect of yearling mass on growth duration for bighorn ewes at Ram Mountain, Alberta. Line indicates the model fitted to the data.

Table 1: Effects of the age at which bighorn ewes reached masses of 40, 50, and 60 kg on their growth rate (kg/day) at these masses at Ram Mountain, Alberta

	Estimates	95% CI	*P* value
Growth rate at 40 kg:			
Intercept	1.24	.403 to 2.08	.004
Age at 40 kg	−.703	−.849 to −.558	<.001
Growth rate at 50 kg:			
Intercept	2.80	1.80 to 3.80	<.001
Age at 50 kg	−.983	−1.14 to −.82	<.001
Growth rate at 60 kg:			
Intercept	5.00	4.00 to 5.99	<.001
Age at 60 kg	−1.33	−1.48 to −1.19	<.001

Note: All estimates are from linear models based on the growth curves of 104 ewes. Age at mass and growth rates were log transformed for all models. CI = confidence interval.

(table 2*A*), explaining 35.9% of its variance. Ewes that were lighter as yearlings grew for a longer duration than heavier ones (fig. 2). Population density and age of primiparity had no significant effects on growth duration (table 2*A*).

Yearling mass was the only fixed effect that affected longevity, accounting for 11.4% of its variance (table 2*B*). Heavier yearlings lived longer, but after yearling mass was accounted for, adult mass and growth duration did not affect longevity (table 2*B*).

Age of primiparity and longevity affected lifetime fecundity (table 2*C*), explaining 82.4% of its variance. Ewes that were primiparous at a younger age and that were long-lived gave birth to more lambs over their lifetime. That result was not unexpected because in the study population after primiparity ewes reproduce almost every year until reproductive senescence (Martin and Festa-Bianchet 2011). Yearling mass, adult mass, population density, and growth duration did not affect fecundity (table 2*C*). By age 4, 87% of ewes had reproduced.

Growth duration, longevity, and population density affected weaning success (table 2*D*), explaining 20.0% of the variance. Ewes that were born at lower density and those with shorter growth durations (fig. 3*A*) weaned a greater proportion of their lambs (table 2*D*). Yearling mass, adult mass, and age of primiparity did not affect weaning success. Of lambs that did not survive to weaning, 66.7% died neonatally: their mother had milk but the lamb was never seen.

Age of primiparity, longevity and growth duration explained 62.3% of the variance in reproductive success (table 2*E*). Ewes that were primiparous at an earlier age and that lived longer had greater lifetime reproductive success. Ewes with shorter growth duration also had greater reproductive success (fig. 3*B*). Adult mass and population density did not affect reproductive success (table 2*E*).

Discussion

In this article, we addressed how survivors of unfavorable early growth deal with trade-offs between growth and reproduction. Our most important finding is that they adopt growth tactics to nearly catch-up by adulthood but at the cost of reduced reproductive success. Although they prolonged growth, ewes that experienced a growth restriction during early development subsequently grew at a slower mass-specific rate than ewes with more rapid early growth, suggesting that poor conditions during early ontogeny had persistent negative effects even among survivors (Pettorelli et al. 2002). We provide insights on why adults of similar size show hitherto unexplained differences in reproduction.

Our results support the contention that ewes have a conservative reproductive strategy, because to prolong growth, lighter ewes appear to divert resources from reproduction (Festa-Bianchet and Jorgenson 1998; Martin and Festa-Bianchet 2010). The fitness benefits of catch-up growth remain unclear. By increasing adult mass, growth prolongation may have a positive effect on survival (Bérubé et al. 1999; Nussey et al. 2011). Although our analyses revealed no positive effect of growth duration on longevity, we could only model growth of individuals that survived to age 7. Therefore, we could only compare relatively long-lived and reproductively successful animals that likely had growth durations near the optimum for their developmental history.

Delayed fitness consequences of early growth restrictions have been reported in numerous taxa (Lindström 1999; Dmitriew and Rowe 2011), but the mechanisms leading to those persistent effects are poorly known. We showed that catch-up growth can conceal life-history trade-offs that cannot be quantified by simple analyses of adult mass. By modeling growth as a continuous process, we quantified trade-offs between growth duration and lamb survival. Catch-up growth was substantial: "light" and "heavy" yearling females differed on average by nearly 20% of mass, but by age 7 they differed by only 4% and overlapped widely in mass (fig. 1). The two groups in figure 1 included the same animals for each analysis, with the exception of one ewe that did not have an estimated mass at age 7. Therefore, catch-up did not result from selective disappearance of smaller individuals (Nussey et al. 2011). Ewes that were light as yearlings prolonged their growth compared to heavy yearlings. We found no evidence of compensatory growth since growth duration was always negatively correlated with mass-specific growth rate. To our knowledge, compensatory growth in mammals has been demonstrated in controlled experiments (Hector and Nakagawa 2012) but rarely in natural systems. Evidence of compensatory growth for wild animals of any

Table 2: Fixed effects affecting growth duration, longevity, lifetime reproductive success, weaning success and lifetime fecundity of bighorn ewes at Ram Mountain, Alberta
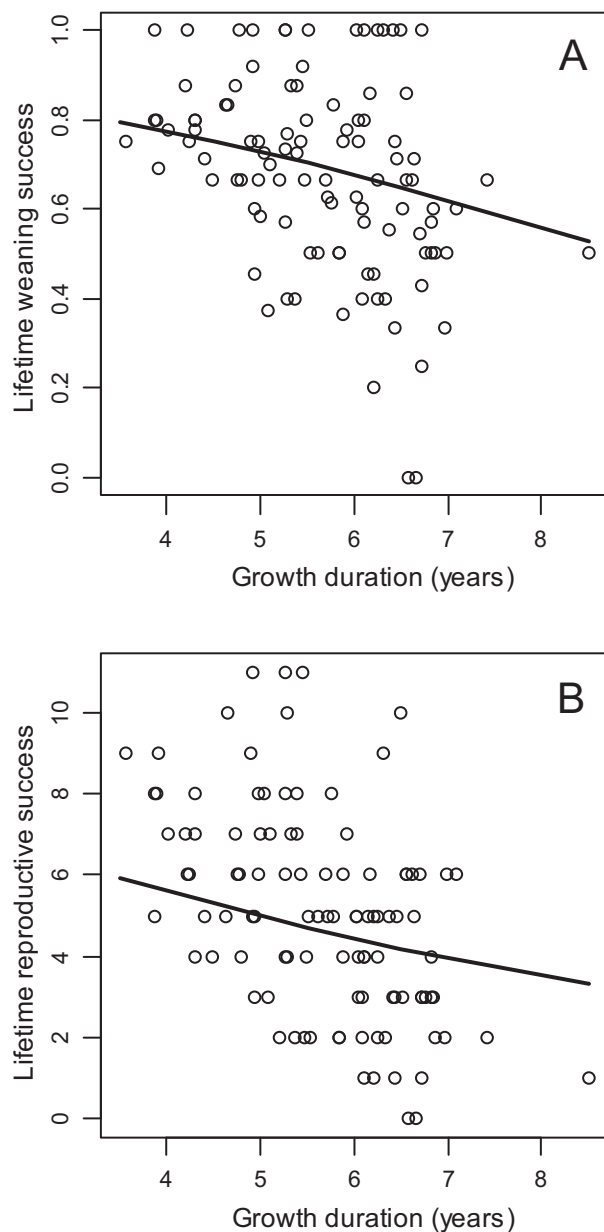
	Estimates	95% CI	P value
A. Growth duration ($n = 85$):			
Full model: yearling mass + population density + age of primiparity			
Final model:			
Intercept	10.536	9.290 to 11.782	<.001
Yearling mass	−.107	−.135 to −.0799	<.001
B. Longevity ($n = 84$):			
Full model: yearling mass + adult mass + growth duration + population density			
Final model:			
Intercept	3.117	−1.478 to 7.711	.187
Yearling mass	.163	.062 to .264	.002
C. Lifetime fecundity ($n = 102$):			
Full model: growth duration + age of primiparity + adult mass + population density + yearling mass + longevity			
Final model:			
Intercept	1.421	.947 to 1.894	<.001
Age of primiparity	−.163	−.247 to −.081	<.001
Longevity	.102	.076 to .127	<.001
D. Lifetime weaning success ($n = 102$):			
Full model: growth duration + age of primiparity + adult mass + population density + yearling mass + longevity			
Final model:			
Intercept	3.589	2.265 to 4.949	<.001
Growth duration	−.251	−.459 to −.046	.017
Population density	−.013	−.022 to −.004	.004
Longevity	−.059	−.115 to −.003	.040
E. Lifetime reproductive success ($n=102$):			
Full model: growth duration + age of primiparity + adult mass + population density + yearling mass + longevity			
Final model:			
Intercept	2.157	1.397 to 2.916	<.001
Growth duration	−.116	−.219 to −.013	.027
Age of primiparity	−.225	−.338 to −.114	<.001
Longevity	.0778	.046 to .109	<.001

Note: *A*, Estimates from a linear mixed model. Year of birth was kept (log likelihood ratio = 15.207, *P* < .001) and maternal identity excluded (log likelihood ratio = 0.611, *P* = .43) as random effects. *B–E*, Estimates from generalized linear models. Year of birth (log likelihood ratio < 0.001, *P* = 1) and maternal identity (log likelihood ratio < 0.001, *P* = 1) were excluded as random effects from all models.

taxon is scarce (but see Johnsson and Bohlin (2006) for a partially controlled experiment). In experiments, growth is usually restricted by limiting food intake (Nicieza and Metcalfe 1997), then providing food ad lib., an unlikely scenario in nature. We suggest that whether or not compensatory growth may occur will largely be determined by the extent of density dependence in fluctuations in resource availability. If food supply varies among years according to environmental changes independent of population density, poor foraging conditions may at times be followed by a period of resource abundance that would allow survivors to accelerate their growth rate (Auer et al. 2012). Experimental manipulations in ectotherms, whose growth can be manipulated by changing ambient temperature (Lee et al. 2012), mimic these conditions. Long-lived endotherms that encounter poor growing conditions early in life because of high intraspecific competition, however, will typically experience those conditions over several

years, making compensatory growth unlikely. That is because changes in population density in these species tend to occur over several years, rather than varying drastically from one year to another (Hamel et al. 2009). In our study, population density in the year of birth was correlated to mean density at ages 1–7 ($r = 0.66$, $P < .001$, $N = 102$). Correlations in environmental conditions across the lifetime should minimize opportunities for compensatory growth and favor growth prolongation.

Growth duration was mostly a function of yearling mass. The considerable effects of population density and age of primiparity were indirect: high density reduces yearling mass, and small yearlings delay primiparity. Yearling mass was density independent at population sizes greater than 60 ewes, likely because of selective mortality of small lambs. When yearling mass was accounted for, however, density did not have any additional effects on growth duration. These results suggest that growth duration was

Figure 3: Variation in weaning success (proportion of lambs born that were weaned; *A*) and lifetime reproductive success (total number of lambs weaned; *B*) of bighorn ewes at Ram Mountain, Alberta, according to their growth duration. Lines indicate models fitted to the data.

that delaying primiparity contributes some of the catch-up growth we observed. There are likely two reasons why we found no effect of age of primiparity on growth duration. First, yearling mass and age of primiparity were correlated ($r = -0.47$, $P < .001$, $N = 83$): much of the variance in growth duration explained by yearling mass was the same as that explained by age of primiparity. Second, 87% of ewes were primiparous by age 4, while growth duration extended beyond 5 years for 74% of ewes, suggesting that primiparity generally occurred before catch-up growth was completed. Catch-up growth extended beyond sexual maturity, suggesting that in addition to a delay in primiparity growth prolongation may involve persisting trade-offs with reproduction. Thus, late primiparity is one of several trade-offs involved in growth prolongation that are ultimately linked to low yearling mass.

We found no evidence of a longevity cost of growth prolongation, likely because rather than high growth rates at any given mass, prolongation involves slow growth over a longer time. Thus, individuals that prolong growth should avoid the metabolic demands of high relative growth rates involved in compensatory growth. Slow growth over a prolonged period may thus be a mechanism to ensure longevity, possibly to the detriment of reproduction. We could assess growth prolongation only in long-lived individuals and found that the lightest yearling ewes had the longest growth durations. Light ewes, however, experience high mortality (Nussey et al. 2011), suggesting that our estimates of the effects of prolonging growth on reproduction are conservative. Although growth duration did not affect fecundity after primiparity, ewes with longer growth durations weaned fewer lambs during their lifetimes because they delayed primiparity and had lower weaning success. In this population, 92% of ewes aged 5–12 years produce a lamb each year. It is therefore unsurprising that catch-up growth did not affect fecundity. The negative effect of growth duration on weaning success suggests a long-term trade-off between growth and reproduction. To prolong growth, ewes may restrain maternal care, reducing lamb mass gain (Festa-Bianchet and Jorgenson 1998; Martin and Festa-Bianchet 2010) and decreasing lamb surviving to weaning (Gallant et al. 2001). Since much of the decrease in lamb survival was due to neonatal mortality, the effects of lower maternal allocation by ewes that prolonged growth may be prenatal, (Blaxter and Hamilton 1980; Landete-Castillejos et al. 2009; Barn-owe-Meyer et al. 2011). The negative effect of longevity on weaning success is likely due to senescence, as reproductive success declines for very old ewes (Martin and Festa-Bianchet 2011).

A recent review found that in several species, the major constraint on growth rate involves a trade-off between predation risk and foraging effort (Dmitriew 2011). Our

mainly determined by a ewe's state relative to an optimal growth trajectory (Metcalfe and Monaghan 2003). Ewes below that optimum prolonged growth regardless of the cause of their growth setback or their reproductive status. Primiparous ewes lost 3.2 kg more during winter and gained 1 kg less during summer than nulliparous ewes of the same age (Martin and Festa-Bianchet 2012), suggesting

research points instead to a longer-term cost of prolonged growth, involving a trade-off with lifetime reproduction. This trade-off may also explain why early environmental constraints on growth can translate into cohort effects (Albon et al. 1987; Hamel et al. 2009). Our detailed analysis based on repeated capture of individuals from the year of birth to adulthood, however, revealed that the effect of growth tactics on other life-history traits can only be quantified by a consideration of multiyear growth patterns. Analyses of growth patterns can explore links between events occurring at different life-history stages, revealing trade-offs that are hidden when analyses are limited to only one life-history stage. The adult phenotype, in particular, is a poor indicator of such trade-offs because catch-up growth, in addition to differential survival (Nussey et al. 2011), weakens its correlation with early growth.

Because growth duration was correlated with yearling mass (fig. 2), it is possible that the fitness costs we measured were partly influenced directly by poor condition during early ontogeny, rather than being only a consequence of a subsequent growth strategy. The slower mass-specific growth rate shown by ewes with poor early growth (table 1) suggests a persistent handicap from a poor early start. Nevertheless, we tried to control for poor conditions during ontogeny by including the potential effects of mass as a yearling and population density in the year of birth in our analyses (table 2). Neither variable had a significant effect on lifetime reproduction. Therefore, we suggest that the negative fitness consequences that we report here are

at least partly the manifestation of a cost of prolonged growth.

Understanding how organisms may cope with fluctuations in environmental conditions is fundamental to our comprehension of the evolution of life-history strategies. Several studies documenting costs of catch-up growth focussed on predation, but very few explored the long-term fitness costs (Dmitriew 2011). By documenting growth patterns of individuals over their lifetime as well as several components of reproductive fitness, we showed how individual differences in ontogeny, which may be hidden in adulthood, can have long-lasting effect on reproductive performance. Thus, to understand diversity in life-history tactics, events occurring in previous life-history stages must be considered.

Acknowledgments

APPENDIX

Table A1: Correlations between variables considered in models

	Growth duration	Yearling mass	Adult mass	Population density	Age of primiparity	Longevity
Growth duration	1	−.66	−.12	.41	.42	−.28
Yearling mass	−.66	1	.38	−.47	−.47	.33
Adult mass	−.12	.38	1	−.29	−.02	.10
Population density	.41	−.47	−.29	1	.54	−.12
Age of primiparity	.42	−.47	−.02	.54	1	−.27
Longevity	−.28	.33	.10	−.12	−.27	1

Note: Correlations are presented for 83 ewes that had data for each variable.

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