Does mass change of primiparous bighorn ewes reflect reproductive effort?

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Abstract: Reproductive effort during a female's first breeding attempt could affect subsequent fitness, particularly in species that reproduce before completing body growth. We analyzed 26 years of data on marked bighorn (*Ovis canadensis*) ewes to assess how variation in first reproductive effort affected other life-history traits. We measured reproductive effort as the residual of the regression of mass of primiparous ewes in late lactation on their mass 1 year earlier. Survival of the first-born lamb to weaning reduced maternal mass gain, suggesting a trade-off between reproduction and growth. Mass gain during the year of primiparity therefore appears to reflect reproductive effort. Lower mass gain was associated with lower adult mass and longevity, two important determinants of lifetime reproductive success. Reproductive effort at first parity therefore appears to lower residual reproductive value. Over their lifetime, females with low mass gain as primiparae produced proportionately more daughters than did females with high mass gain. Reproductive effort at first reproduction was not heritable, and may affect the evolutionary potential of adult mass and longevity, two fitness-related traits that are highly heritable in the study population.

Résumé : L'effort à la première reproduction peut affecter la valeur adaptative ultérieure des femelles, particulièrement chez les espèces dont la croissance se poursuit après la maturité sexuelle. A partir de l'analyse de 26 années de données sur des femelles marquées de Mouflons d'Amérique (*Ovis canadensis*), nous avons vérifié de quelle manière l'effort reproducteur affectait d'autres traits d'histoire de vie. L'effort de reproduction est défini comme le résidu de la régression de la masse de chaque brebis primipare sur sa masse l'année précédente. La survie au sevrage du premier agneau réduisait le gain de masse de la brebis durant sa première reproduction, ce qui suggère l'existence d'un compromis entre la reproduction et la croissance. Le gain de masse lors de la première reproduction semble donc refléter l'effort reproducteur. Un gain de masse limité correspond à une masse plus faible chez l'adulte et à une longévité réduite, deux facteurs déterminants de la fécondité et de la contribution reproductrice totale. L'effort à la première reproduction semble donc réduire la valeur reproductrice résiduelle. Les femelles primipares dont le gain de masse est réduit produisent relativement plus d'agnelles au cours de leur vie que celles ayant un gain de masse élevé. L'effort à la première reproduction n'est pas héritable et pourrait affecter le potentiel évolutif de la masse adulte et de la longévité, deux caractères associés à la valeur adaptative et fortement héritables chez la population d'étude.

Introduction

Females with continued somatic growth after sexual maturity face a trade-off between reproductive effort at first breeding and body growth (Roff 1992; Stearns 1992). Body size is usually associated with fitness traits (Hewison 1996; Festa-Bianchet et al. 1997, 1998), and life-history theories have recognized the selective importance of attaining sexual maturity at an optimal age and size (Gadgil and Bossert 1970). Studies of mammals have examined the correlates (Jorgenson et al. 1993; Langvatn et al. 1996; Sæther et al. 1996) or the fitness consequences of the age of primiparity (Lunn et al. 1994; Festa-Bianchet et al. 1995). Regardless of age, however, reproductive effort at first breeding should reduce the amount of body reserves available for growth and

maintenance, potentially reducing residual reproductive value (Williams 1966; Tuomi et al. 1983). Little is known about the fitness consequences of reproductive effort at first breeding, partly because of the difficulty of measuring reproductive effort and of obtaining life-history data for known individuals.

We analyzed 26 years of longitudinal data on marked bighorn (*Ovis canadensis*) ewes, to assess the fitness consequences of mass change during the year of primiparity. For each primiparous female, we measured mass change from 2 months before conception to 1 year later, which corresponds to the approximate time of weaning of the first lamb. Most ewes gained mass during this period. Bighorn ewes can reproduce 2–5 years before they reach adult mass (Jorgenson et al. 1993). Females breed in late autumn and give birth to one lamb after a 6-month gestation, followed by a 4-month lactation. The competing demands of growth and reproduction and the fixed litter size make bighorn ewes particularly suitable for the study of initial reproductive effort.

We asked three questions. (1) Is mass gain of primiparae related to weaning success? A negative relationship would suggest that lamb survival to weaning decreases the female's subsequent growth. Lactation is the most energetically demanding component of reproduction for female mammals (Gittleman and Thompson 1988). (2) Is mass gain during the year of primiparity related to fitness? We considered three

fitness traits: adult mass, longevity, and lifetime fecundity (lambs produced). A positive relationship between mass gain and fitness traits would indicate long-term consequences of an initial growth deficit. (3) Is there a relationship between mass gain during primiparity and the sex ratio of offspring? Trivers and Willard (1973) proposed that, if the level of maternal expenditure affects the fitness of one sex more than the other, females in good condition should produce more offspring of the most-affected sex. In bighorn sheep, male reproductive success is very variable and largely dependent upon body size (Hogg and Forbes 1997), while females only produce one lamb a year. Thus, if low mass gain indicated high initial reproductive effort, we expected that ewes that gained little mass during primiparity would have a female-biased offspring sex ratio later in life.

Materials and methods

The study population inhabits Ram Mountain (52°N, 115°W, elevation 1082–2173 m asl), Alberta. Yearly multiple captures of almost every ewe were made in a corral trap baited with salt from late May to early October, 1973–1998. All adult ewes were marked from 1976 onward. Ewes were identified by canvas collars and lambs by Ketchum metal ear tags and coloured strips of Safeflag plastic. A spring scale was used to weigh sheep to within 250 g. Female reproductive status was determined by udder examination to be either barren, pregnant, lactating, or having lost their lamb. During field observations, ewes nursing a lamb were considered to be lactating. Festa-Bianchet et al. (1995) provide further details on capture methods. The protocol was approved by the Animal Care Committee of the Université de Sherbrooke.

A removal experiment between 1972 and 1981 held adult ewe numbers at 30–34. The cessation of removals led to a threefold increase in the number of adult ewes. With increasing density, ewe fecundity decreased and the costs of reproduction increased (Festa-Bianchet et al. 1998), weaning mass decreased (Festa-Bianchet and Jorgenson 1998), lamb mortality increased (Portier et al. 1998), horn growth in young males was reduced (Jorgenson et al. 1998), and primiparity was delayed (Jorgenson et al. 1993). These multiple lines of evidence suggest that food was scarce at high density.

Female body mass was adjusted to 15 September. The mass of sheep captured more than once in a season was adjusted using individual rates of mass gain. The mean rate of summer mass gain from all ewes of the same age and reproductive status was used to adjust mass for females caught only once in a summer. More details about mass adjustments are provided in Festa-Bianchet et al. (1996). We defined adult body mass as the average mid-September mass of each ewe from 5 to 10 years of age after adjusting for age effects.

A total of 120 females born between 1973 and 1991 that survived at least 5 years were used for analyses of mass gain. For analyses of longevity, fecundity, lifetime reproductive success, and offspring sex ratio, we used a subset of 92 females born between 1976 and 1989. For these females, we knew age and mass at primiparity, longevity, lifetime fecundity, and reproductive success. Thirteen females in this subset were still alive in 1998, but all were at least 9 years of age, older than the mean longevity (7.1 years) of ewes that survived to 1 year of age and died of natural causes.

Data analysis

Mating occurs in late November and early December (Hogg and Forbes 1997). Ewe mass on 15 September is representative of mass during the rut, as little mass accumulation takes place after September (Festa-Bianchet et al. 1996). Mid-September is also the approximate time of weaning (Festa-Bianchet 1988). Thus, our measure of mass gain during primiparity was the residual of the regression of mass in the mid-September before first conception and mass in the mid-September following first lambing (Fig. 1). This measure of mass gain was independent of mass in the mid-September before first conception. Bighorn ewes gain mass until they are at least 6 years of age (Festa-Bianchet et al. 1996).

We used generalized linear models (GLMs) (McCullagh and Nelder 1989), first to analyze whether age and mass at primiparity, population density (the number of adult ewes in June), and weaning success at first breeding (coded 0 for failure and 1 for success) affected variation in mass gain during the year of primiparity and, secondly, to explore the relationship between mass gain and fitness components. We used age and mass at primiparity as covariates in analyses of adult mass. Density was not included because it does not affect the adult mass of ewes (Festa-Bianchet et al. 1998). For other traits, age and mass at primiparity and population density were used as covariates. We also analyzed the effect of mass gain during the year of primiparity on offspring sex ratio. The number of sons produced during a female's lifetime was the dependent variable, with the number of daughters produced (a measure of overall reproductive success), age and mass at primiparity, and mass gain as covariates.

Mass gain and adult mass were normally distributed (Shapiro–Wilk test: $W = 0.67$, $p = 0.08$ and $W = 0.969$, $p = 0.13$, respectively). Normal error distribution and an identity link function (McCullagh and Nelder 1989) were therefore used for the GLM on these traits. Poisson error distribution and a logarithmic link function were used for GLM analyses of longevity, fecundity, and number of sons produced. Model selection was by backward deletion: each variable and higher order interactions were removed one by one from the model (see Festa-Bianchet et al. (1998) for a detailed description of this procedure). Significance was assessed by a likelihood ratio test of the difference in deviance of models with and without a variable, which approximates a χ^2 distribution with degrees of freedom equal to the difference in the number of parameters in the two models. The general model contains all significant variables and interactions. When an interaction was significant, the main effects composing it were included in the selected model, even if they were not significant when considered alone. We estimated the proportion of variation explained by the model as (Dev1 – Dev2)/Dev1, where Dev1 is the deviance of the null model and Dev2 is the deviance of the general model (Schemper 1990; Festa-Bianchet et al. 1998). For fecundity, we analyzed models with and without longevity because longevity affects variation in female fecundity (Bérubé et al. 1999). Among the traits used as covariates in GLMs, age and mass at primiparity had the highest correlation ($r = 0.70$), followed by age at primiparity and fecundity ($r = -0.47$). All other variables were weakly correlated ($r < 0.40$). GLM analyses were conducted with S-Plus 2000 (Mathsoft Inc., Seattle, Wash.).

Narrow-sense heritability (h^2) of mass gain during the year of primiparity was estimated by the offspring–parent regression method (Falconer and Mackay 1996), regressing the mean value of daughters on the value of mothers. Heritability is the slope of the regression multiplied by two, and standard error of heritability is twice the standard error of the slope (Falconer and Mackay 1996).

Results

Body mass before first reproduction was correlated with mass 1 year later (Fig 1), but half the variability in mass after first reproduction was independent of mass just before first conception ($r^2 = 0.48$, $F_{[1,118]} = 109.78$, $p < 0.0001$). Only 9.7% of the variation in mass gain during first reproduction was accounted for by weaning success and population density (Table 1). Ewes that weaned their first lamb

Fig. 1. Mass on 15 September before primiparity and mass
1 year later, for bighorn ewes at Ram Mountain, Alberta, 1976–
1998. Different symbols indicate ewes of different ages at
primiparity. The residuals of this regression were used to mea-
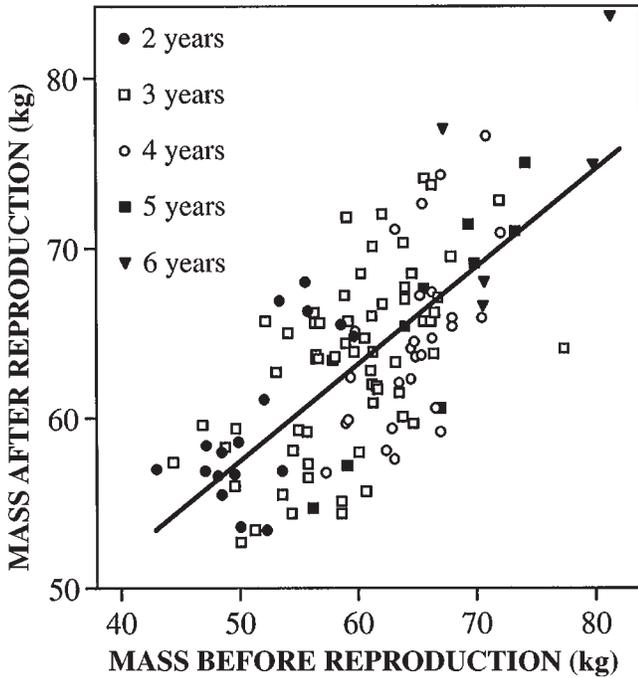sure mass gain during primiparity.

Table 1. Generalized linear model selection for re-
sidual mass change during year of first reproduction
(MC) for bighorn sheep ewes at Ram Mountain
from 1973 to 1998.

(A) General model: MC = AP × D × WS

Variables	F ratio	df	P
AP·D·WS	0.192	1,112	0.662
AP·WS	3.142	1,113	0.079
D·WS	2.557	1,113	0.113
AP·D	0.779	1,113	0.379
AP	0.004	1,116	0.947
D	3.701	1,116	**0.057**
WS	9.701	1,116	**0.003**

(B) Selected model: MC = D + WS

Variable	Estimate	SE
D	–0.040	0.018
WS	–2.699	0.878

Note: AP is age at primiparity, D is population density,
WS is weaning success at first breeding, X × Y is the
cumulative effects of the variables, as well as their
interaction, and X·Y is the interaction between X and Y.
Significant P values are shown in bold.

Table 2. Generalized linear model selection for
adult mass (ADM) of bighorn ewes at Ram Moun-
tain from 1976 to 1998.

(A) General model: ADM = AP × MP × MC

Model	F ratio	df	P
AP·MP·MC	2.727	1,84	0.102
MP·AP	7.500	1,85	**0.008**
MC·AP	4.405	1,85	**0.039**
MC·MP	5.260	1,85	**0.024**
AP	12.644	1,85	**<0.001**
MP	0.0039	1,85	0.950
MC	4.189	1,85	**0.044**

**(B) Selected model: ADM = AP + MP + MC +
AP·MC + AP·MP + MP·MC**

Variables	Estimate	SE
AP	–12.840	3.611
MP	0.186	0.186
MC	2.104	1.028
MC·AP	0.368	0.175
MC·MP	–0.052	0.022
AP·MP	0.147	0.054

Note: MC is residual mass change during the year of
first reproduction, AP is age at primiparity, MP is mass on
15 September the year before primiparity, X × Y is the
cumulative effects of the variables, as well as their
interaction, and X·Y is the interaction between X and Y.
Significant P values are shown in bold.

gained less mass than those that failed to do so, and density
limited mass gain during first breeding.

Several variables were correlated with adult mass (Table 2).
The selected model explained 39% of the variation in adult
mass. Both mass gain during the year of first reproduction

and mass in the mid-September before primiparity were re-
lated to adult mass, and their effect was most evident for
ewes that became primiparae at an advanced age (Table 2).
Mass gain during the year of first reproduction had a posi-
tive effect on adult mass, particularly for ewes that were rel-
atively light in the mid-September before they first
reproduced (Table 2).

Ewes that gained more mass during the year of first repro-
duction lived longer than ewes with a lower mass gain
(Fig. 2). Mass gain explained 20.7% of the variation in lon-
gevity, while population density, mass in the mid-September
before primiparity, and age at primiparity had no effect (Ta-
ble 3). Lifetime fecundity increased with mass gain during
the year of first reproduction and was negatively related to
age at primiparity (Table 4). As expected for a species that
can only produce one offspring each year, fecundity was
strongly related to longevity (null GLM deviance = 150.791;
general model deviance = 28.303; likelihood ratio test =
122.488, df = 1, p < 0.0001) and to its second order poly-
nomial (likelihood ratio test = 9.5, df = 1, p < 0.001). There-
fore, fecundity increased with longevity at a declining rate
(Table 4). However, when the effects of longevity on fecun-
dity were accounted for, mass gain during the year of first
reproduction did not affect fecundity (Table 4). Models with
and without longevity explained 93.1 and 39.1% of the vari-
ation in fecundity, respectively.

The number of sons produced by each ewe increased with
both the number of daughters produced and mass gain dur-
ing the year of first reproduction (Table 5), suggesting an in-
creasing bias in sex ratio towards male lambs for ewes that
reduced reproductive effort at first breeding (Fig. 3). The

Fig. 2. The relationship between mass change during the year of first reproduction (the residuals of the regression of mass on 15 September the year before primiparity and mass 1 year later) and longevity for bighorn ewes at Ram Mountain, Alberta, 1976–1998.
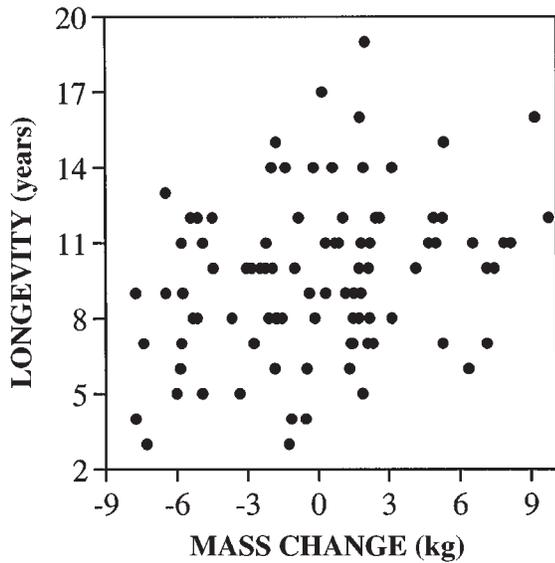

Fig. 3. Mass change during the year of first reproduction and the proportion of sons among lambs of known sex produced over their lifetime for bighorn ewes at Ram Mountain, Alberta, 1976–1998.
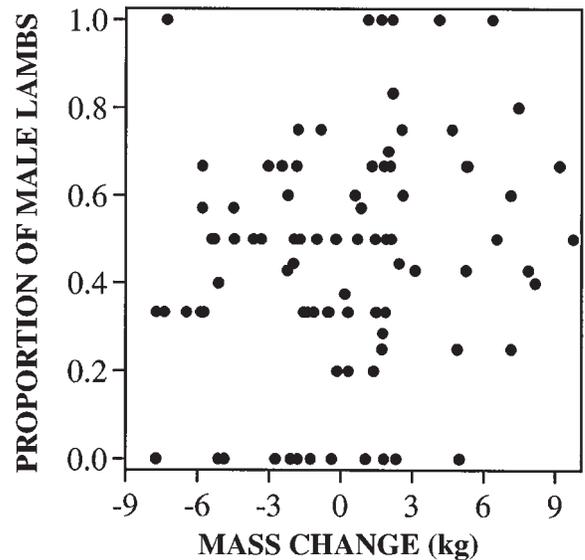

Table 3. Generalized linear model selection for longevity (LG) of bighorn ewes at Ram Mountain from 1976 to 1998.

(A) Model selection

			Model comparisons			
Model	Deviance	df	Models compared	Difference in deviance	Difference in df	P (likelihood ratio test)
1. Null model	96.501	91				
2. General model: LG = AP × MC × D × MP	76.569	76	1 and 2	19.932	15	<0.001
3. LG = Eq. 2 – (AP·MC·D·MP)	76.588	77	3 and 2	0.019	1	>0.05
4. LG = AP + MP + D + MC + AP·MP + AP·D + MP·D + AP·MC + MP·MC + D·MC	78.353	81	4 and 3	1.765	4	>0.05
5. LG = AP + MP + D + MC	84.688	87	5 and 4	6.335	6	>0.05
6. LG = Eq. 5 – MC	90.555	88	6 and 5	5.867	1	**<0.01**
7. LG = Eq. 5 – D	84.796	88	7 and 5	0.108	1	>0.05
8. LG = Eq. 5 – MP	84.948	88	8 and 5	0.260	1	>0.05
9. LG = Eq. 5 – AP	86.611	88	9 and 5	1.923	1	>0.05

(B) Model selected: LG = MC

Variable	Estimate	SE
MC	0.023	0.008

Note: Interactions were removed one by one from the model and their significance tested individually; those that were not significant are not shown. MC is residual mass change during the year of first reproduction, AP is age at primiparity, MP is mass on 15 September the year before primiparity, D is population density, X × Y is the cumulative effects of the variables, as well as their interaction, and X·Y is the interaction between X and Y. Significant P values are shown in bold.

model explained 33.2% of the variation in number of sons produced by each ewe. Heritability of mass gain during the year of first breeding was low and not significantly different from zero ($h^2 = -0.09 \pm 0.32$ SE, $n = 37$ families).

Discussion

Ewes that weaned their first lamb gained less mass than those whose first lamb died before weaning, suggesting a phenotypic trade-off between reproduction and growth for primiparous bighorn ewes, likely caused by the energetic cost of lactation. Mass gain during the year of first reproduction decreased at high density. These results suggest that mass gain during the year of first reproduction is an index of initial reproductive effort in bighorn ewes.

Our results also support the hypothesis that an increase in initial reproductive effort reduces residual reproductive value. Poizat et al. (1999) found indirect evidence of a trade-off between effort at first breeding and residual reproductive value. They showed that, in females of the multispawning stickleback (*Gaterosteus aculeatus*), lower mass gain at first breeding was associated with a shorter life span. Light

Table 4. Generalized linear model selection for fecundity (FEC) of bighorn ewes at Ram Mountain from 1976 to 1998.

(A) Model selection

Model	Deviance	df	Models compared	Difference in deviance	Difference in df	*P* (likelihood ratio test)
1. Null model	150.791	89				
2. General model: FEC = AP × MC × D × MP	91.767	74	1 and 2	59.024	15	<0.001
3. FEC = Eq. 2 – (AP·MC·D·MP)	91.778	75	3 and 2	0.011	1	>0.05
4. FEC = AP + MP + D + MC + AP·MP + AP·D + MP·D + AP·MC + MP·MC + D·MC	92.850	79	4 and 3	1.072	4	>0.05
5. FEC = AP + MP + D + MC	104.038	85	5 and 4	11.26	6	>0.05
6. FEC = Eq. 5 – MC	110.859	86	6 and 5	6.82	1	**<0.05**
7. FEC = Eq. 5 – D	104.614	86	7 and 5	0.576	1	>0.05
8. FEC = Eq. 5 – MP	105.312	86	8 and 5	1.274	1	>0.05
9. FEC = Eq. 5 – AP	119.631	86	9 and 5	15.593	1	**<0.001**

(B) Model selected: FEC = MC + AP

Variable	Estimate	SE
AP	–0.279	0.052
MC	0.030	0.010

(C) Model selected when LG and LG2 were included: FEC = LG + LG2 + AP

Variable	Estimate	SE
LG	0.364	0.071
LG2	–0.011	0.003

Note: Interactions were removed one by one from the model and their significance tested individually; those that were not significant are not shown. MC is residual mass change during the year of first reproduction, AP is age at primiparity, MP is mass on 15 September the year before primiparity, D is population density, LG is longevity, LG2 is the square of age at death, X × Y is the cumulative effects of the variables, as well as their interaction, and X·Y is the interaction between X and Y. Significant *P* are shown in bold.

Table 5. Generalized linear model selection for number of sons produced (ML) by bighorn ewes at Ram Mountain from 1976 to 1998.

(A) Model selection

Model	Deviance	df	Models compared	Difference in deviance	Difference in df	*P* (likelihood ratio test)
1. Null model	116.340	87				
2. General model: ML = FL + AP × MC × D × MP	77.729	71	1 and 2	38.611	16	<0.001
3. ML = Eq. 2 – (AP·MC·D·MP)	78.442	72	3 and 2	0.713	1	>0.05
4. ML = FL + AP + MP + D + MC + AP·MP + AP·D + MP·D + AP·MC + MP·MC + D·MC	79.578	76	4 and 3	1.136	4	>0.05
5. ML = FL + AP + MP + D + MC	87.512	82	5 and 5	7.934	6	>0.05
6. ML = Eq. 5 – MC	92.989	83	6 and 5	5.477	1	**<0.01**
7. ML = Eq. 5 – D	87.639	83	7 and 5	0.127	1	>0.05
8. ML = Eq. 5 – MP	87.541	83	8 and 5	0.029	1	>0.05
9. ML = Eq. 5 – AP	90.810	83	9 and 5	3.298	1	>0.05
10. ML = Eq. 5 – FL	91.759	83	10 and 5	4.247	1	**<0.05**

(B) Model selected: ML = FL + MC

Variable	Estimate	SE
FL	0.178	0.053
MC	0.046	0.018

Note: Interactions were removed one by one from the model and their significance tested individually; those that were not significant are not shown. In these models, number of daughters produced per ewe (FL) is considered a covariate. MC is residual mass change during the year of first reproduction, AP is age at primiparity, MP is mass on 15 September the year before primiparity, D is population density, X × Y is the cumulative effects of the variables, as well as their interaction, and X·Y is the interaction between X and Y. Significant *P* values are shown in bold.

bighorn ewes do not live as long as heavy ones (Bérubé et al. 1999), and the relationship between mass gain during the year of first reproduction and longevity could be due to an effect of mass gain on adult mass. Indeed, the negative effect of low mass gain at first breeding on adult mass was most evident for small primiparae and for ewes that first reproduced at an advanced age.

Precocious females, or females that attained primiparity at high body mass, were likely better able to afford the growth cost of first reproduction than late or small primiparae. Reproductive effort, therefore, varied according to both the quantity of resources allocated to first reproduction and the total level of resources available. The stronger relationship between mass at primiparity and adult mass for late primiparae was expected because the later ewes reproduce the closer they are to their asymptotic mass. Confirming previous results (Jorgenson et al. 1997), longevity was not affected by age or mass at primiparity or by population density.

Lower mass gain during the year of first breeding was associated with reduced fecundity. Once differences in longevity were accounted for, however, fecundity was not compromised by initial reproductive effort. Therefore, initial reproductive effort may affect residual reproductive value indirectly by reducing longevity (Stearns 1992).

Late primiparae experienced lower fecundity than ewes that first reproduced at a younger age, and fecundity increased with ewe longevity. Because ewes can only produce one lamb per year, the duration of the reproductive lifespan is an important determinant of lifetime reproductive success. The curvilinear relationship of longevity and fecundity can be attributed to reproductive senescence (Bérubé et al. 1999).

The suggestion that phenotypic variation in initial reproductive effort could affect fitness is also supported by the correlation of mass gain during first reproduction and offspring sex ratio. Studies of ungulates have produced inconsistent results regarding the relationship between maternal condition and offspring sex ratio (Kojola 1998). Bighorn ewes with a greater effort at first breeding produced a slightly higher proportion of daughters over their lifetime. Sons are costlier to raise than daughters (Bérubé et al. 1996). Therefore, high somatic costs of first reproduction may cause females to adjust subsequent offspring sex ratio to avoid producing the costlier sex or may increase the neonatal mortality of sons produced by these ewes.

What could be the evolutionary consequences of variation in initial reproductive effort? The genetic variability of traits strongly associated with fitness should be eroded by selection (Fisher 1930). Adult mass is related to fitness in the Ram Mountain population (Festa-Bianchet et al. 1997, 1998; Bérubé et al. 1999), yet it shows substantial heritability (0.60) that indicate high additive genetic influences on its phenotypic variation (Réale et al. 1999). On the contrary, the heritability of mass gain at first breeding is not significant, suggesting that most variation in initial reproductive effort is environmental. The trade-off between first breeding and growth may, therefore, represent an ecological rather than an evolutionary cost of reproduction (Reznick 1985). The positive relationships between mass gain and adult mass or longevity are probably not due to high genetic correlations because such correlations require both traits to be heritable (Falconer and Mackay 1996).

Our results have two general implications for our understanding of the selective pressures on initial reproductive effort and for the consequences of reproductive effort on fitness traits. First, the low heritability of reproductive effort may be attributed to a strong selective effect on this trait (Fisher 1930) that affects the residual reproductive value of females. Second, mass gain during the year of first reproduction can affect longevity and adult mass, which, in turn, affect fecundity and lifetime reproductive success. Initial reproductive effort may, therefore, contribute to the decrease in the evolutionary potential of adult mass and longevity, two traits that are highly associated with fitness.

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