

Mass-dependent reproductive strategies in wild bighorn ewes: a quantitative genetic approach

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Abstract

In the Ram Mountain bighorn sheep (*Ovis canadensis*) population, ewes differing by more than 30% in body mass weaned lambs with an average mass difference of only 3%. Variability in adult body mass was partly due to additive genetic effects, but inheritance of weaning mass was weak. Maternal effects could obscure genetic effects in the phenotypic expression of weaning mass, particularly if they reflected strategies of maternal expenditure that varied according to ewe mass. We performed a quantitative genetic analysis to assess genetic and environmental influences on ewe mass and on maternal expenditure. We used the mean daughters/mother regression method and Derivative Free Restricted Maximum Likelihood models to estimate heritability (h^2) of ewe mass and indices of maternal expenditure. We found additive genetic effects on phenotypic variation in maternal mass, in lamb mass at weaning (absolute maternal expenditure) and in weaning mass relative to maternal mass at weaning (relative maternal expenditure). Heritability suggests that maternal expenditure has the potential to evolve. The genetic correlation of ewe mass and absolute maternal expenditure was weak, while ewe mass and relative maternal expenditure were strongly negatively correlated. These results suggest additive genetic effects on mass-dependent reproductive strategies in bighorn ewes. Mass-dependent reproductive strategies could affect lamb survival and phenotypic variation in adult mass. As population density increased and reproduction became costlier, small females reduced maternal expenditure more than large females. Constraints on reproductive strategy imposed by variations in resource availability are therefore likely to differ according to ewe mass. A general trend for a decrease in maternal expenditure relative to maternal size in mammals suggests that size-dependent negative maternal effects may be common.

Introduction

The evolution of reproductive strategies and of parental care has been the object of much theoretical and empirical work (Trivers, 1972; Clutton-Brock, 1991). Parental care has been the focus of many behaviour studies, but of few quantitative genetic studies, despite the potential contribution that a genetic approach could

make to our understanding of the evolution of parental care strategies (Cheverud & Moore, 1994). To evolve, parental care must have some heritable genetic variation (Cheverud & Moore, 1994; Shaw & Byers, 1998). The evolutionary potential of a quantitative character is given by its heritability (h^2), or the proportion of its phenotypic variance among individuals in a population due to additive genetic variance (Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998). Heritability has been estimated for several parental attributes: significant heritability has been found for clutch size (van Noordwijk *et al.*, 1981a; Findlay & Cook, 1983; Schluter & Gustafsson, 1993; see Roff, 1992, for a review), litter size

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(Meyer *et al.*, 1994; Ap Dewi *et al.*, 1996; Alfonso *et al.*, 1997), and egg size in a variety of taxa (Larsson & Forslund, 1992; Sinervo & Doughty, 1996; reviewed by Roff, 1992, 1997). The timing of reproduction can also be heritable (van Noordwijk *et al.*, 1981b; Findlay & Cook, 1982; Sinervo & Doughty, 1996), and heritabilities of weight loss during lactation (Hansen & Berg, 1998) and of milk production have been shown in domestic mammals (Suzuki & Van Vleck, 1994; Sanna *et al.*, 1997). Little is known, however, about the quantitative genetics of parental expenditure (Cheverud & Moore, 1994), except for a few studies of heritability of paternal investment in insects (Sakaluk & Smith, 1988; Savalli & Fox, 1998).

Parental attributes are generally considered maternal effects, where a parent's phenotype or environment affect the expression of phenotypic characters in the offspring (Mousseau & Dingle, 1991; Bernardo, 1996; Mousseau & Fox, 1998a,b; Wolf *et al.*, 1998). The term 'maternal effects' is generally used because of the predominance of the mother's nongenetic effects on offspring phenotype, but it includes maternal, paternal and other kin effects (Cheverud & Moore, 1994; Rossiter, 1996; Wolf *et al.*, 1998). Several theoretical studies have illustrated the potential role of maternal effects in the evolution of polygenic traits (Cheverud, 1984; Lynch, 1987; Kirkpatrick & Lande, 1989; Lande & Kirkpatrick, 1990). Maternal effects can accelerate or dampen the rate of evolution of characters, change the direction of evolution, and even induce maladaptive responses to selection (Kirkpatrick & Lande, 1989; Lande & Kirkpatrick, 1990; Wolf *et al.*, 1998).

Here we investigate the heritability of maternal expenditure within the bighorn sheep (*Ovis canadensis*) population on Ram Mountain, Alberta, from 1973 to 1998. Festa-Bianchet & Jorgenson (1998) reported a very weak relationship between a ewe's and her lamb's body mass at weaning. As population density increased, lamb mass gain during summer decreased much more than mass gain by lactating ewes, suggesting that females adopted a conservative reproductive strategy and favoured their own mass gain over their lamb's. Heritability estimates of body mass were low to intermediate (0.00–0.43) before 3 years of age and intermediate to high (0.23–0.81) for older sheep (Réale *et al.*, 1999). The increase in heritability of morphological characters during ontogeny is generally associated with declining maternal effects with age (Cheverud, 1984; Rossiter, 1996). We could not estimate maternal effects and direct-maternal covariance because sires were unknown, and we suggested that a negative maternal effect could cause an underestimation of heritability of body mass early in life. Small ewes may produce genetically small lambs and large ewes may produce genetically large lambs, but given the higher maternal expenditure of small ewes compared with large ones (Festa-Bianchet & Jorgenson, 1998), small and large females may wean lambs of similar

mass. In this paper, we assess whether absolute and relative maternal expenditure are heritable. We define maternal expenditure as the amount of resources (energy or time) devoted by a mother to her offspring independent of fitness costs for the mother (Clutton-Brock, 1991). We examined both absolute maternal expenditure, estimated by lamb mass at weaning, and relative maternal expenditure, the proportion of total ewe mass devoted to offspring. These indices can be considered as one component of maternal expenditure.

Because of the very weak relationship between mother and offspring mass near the time of weaning, we also assessed whether maternal care strategies may be genetically related to female mass. Therefore, we estimated genetic correlations between maternal expenditure indices and ewe mass. Genetic correlation, generally due to pleiotropy or to linkage disequilibrium, indicates the degree to which two continuous traits are genetically related (Falconner & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998). Because traits that are strongly correlated cannot evolve independently (Lande & Arnold, 1983; Price & Langen, 1992), a quantitative genetic study may provide clues to the evolution of mass-dependent reproductive strategies.

Because as density increased lamb mass decreased much more than ewe mass, and because relative maternal expenditure varied according to ewe mass (Festa-Bianchet & Jorgenson, 1998), we expected that maternal expenditure of small ewes would be more affected by density than the expenditure of large ewes. Small ewes experience greater fitness costs of reproduction than large ewes (Festa-Bianchet *et al.*, 1998). To test this prediction, we examined how weaning mass changed for the lambs of individual ewes with increasing density, and compared these changes for ewes differing in body mass.

Methods

Data used in this paper were collected on Ram Mountain, Alberta (52°N 115°W; elevation 1082–2173 m) between 1973 and 1998. Until 1981, yearly ewe removals limited the population to 30–33 adult ewes. Removals ended in 1981, the population increased and peaked at 104 ewes in 1992, then declined to 75 ewes by 1997 and 54 in 1998, following removal of 11 adult ewes in 1997.

Each summer, about 90% of adult ewes were captured 2–6 times and weighed to the nearest 125 g with a Detecto spring scale. Body mass was adjusted to 15 September using each individual's own rate of summer mass gain obtained from multiple captures. Festa-Bianchet *et al.* (1997) provide more details on capture schedule and on mass adjustments. In most years, over 80% of lambs were captured and marked before October, and mother–lamb relationships were assessed by observations of suckling and other maternal behaviours.

Unmarked lambs that survived the winter were marked the following year, but their mothers could not be identified. Lambs were more difficult to capture than adult ewes, and therefore for lambs captured only once we adjusted mass using the mean rate of mass accumulation for lambs of the same sex weighed at least twice in that same year. To increase the accuracy of heritability estimates, we statistically removed environmental effects on phenotypic variance. Lamb mass was first standardized according to sex $[(x_i - \text{mean})/\text{SD}]$ where x_i is the individual value of body mass; mean mass for males = 28.3 ± 4.7 kg, $N = 187$ and for females = 25.7 ± 4.1 kg, $N = 179$. To account for year-to-year differences in lamb mass due to the effects of climate and population density, we used year-specific residuals to adjust lamb mass to the mean estimate for 1989. To account for the effects of age, climate and population density on ewe mass, we adjusted maternal mass to the mean estimate for 7-year-old ewes in 1989.

Indices of maternal expenditure

Lamb mass adjusted to 15 September corresponds approximately to weaning mass and is partly a function of maternal expenditure (Festa-Bianchet & Jorgenson, 1998). Therefore, lamb mass can be used as an index of absolute maternal expenditure. To assess relative maternal expenditure, we calculated the ratio of lamb mass on ewe mass, based on the assumption that a higher ratio would result from a greater proportion of total maternal resources being devoted to reproduction. The nature of the relationship between relative maternal expenditure and maternal mass would depend on the pattern of covariation of offspring mass and maternal mass: if relative maternal expenditure increased with maternal mass, then offspring mass would increase faster than maternal mass and the slope of the regression of relative expenditure on maternal mass would be >1 . If relative maternal expenditure was independent of body mass, then offspring mass and maternal mass would increase at the same rate (slope = 1). Finally, if relative maternal expenditure and maternal mass were negatively correlated, then offspring mass may increase less rapidly than maternal mass, be independent of it, or decrease with increasing maternal mass (slope <1). Thus, the phenotypic correlation between relative maternal expenditure and maternal mass will depend on the form of the relationship between offspring mass and maternal mass. The genetic correlation will depend on both this relationship and the heritability of absolute maternal expenditure and maternal mass.

Quantitative genetic parameters

For all analyses, pedigrees were based on mother–lamb relationships established in the field. Sires were unknown and therefore we could not estimate heritability by using

sire–offspring relationships. Because only 7.3% of 101 lambs of 36 ewes (reproductive events per ewe: mean = 3; range 2–6) were full-sibs in another bighorn sheep population (Sheep River; J. T. Hogg, unpublished data), and because of the high mortality of adult rams (Jorgenson *et al.*, 1997), we assumed that offspring of the same female were half-sibs. There is little possibility for a common early environment to have different effects on different family groups and therefore affect heritability estimates, because bighorn ewes always produce singletons, are highly phylopatric, do not form kin groups and all ewes in the population use the same home range (Festa-Bianchet, 1991).

Heritability was estimated for ewe mass, absolute maternal expenditure and relative maternal expenditure. Ewe mass and absolute maternal expenditure were normally distributed (Shapiro–Wilk W -test; ewe mass: $P = 0.99$; absolute maternal expenditure: $P = 0.99$). Relative maternal expenditure was arcsine-transformed before analyses. Values for ewe mass, absolute maternal expenditure and relative maternal expenditure were analysed for ewes and their daughters, including all available records for females aged 3–16 years. We compared the adult mass of ewes and their daughters, and considered maternal expenditure indices as mother traits. For absolute maternal expenditure, the average weaning mass of the lambs of each ewe was compared with the average weaning mass of her daughters' lambs. For relative maternal expenditure the average ratio of lamb mass on ewe mass for each female was compared with the same ratio for each ewe's daughters.

We first estimated heritabilities and genetic correlations using the mean daughters/mother regression method (Falconner & Mackay, 1996). For each trait, the mean value of daughters was regressed on the value of mothers. Heritability is the slope of the regression multiplied by 2, and its standard error is twice the standard error of the coefficient of the regression (Falconner & Mackay, 1996). Additive genetic correlations (r_a ; genetic correlations below) were estimated from the arithmetic mean between correlation coefficients $r = \text{cov}_{XY} / \sqrt{(\text{cov}_{XX}\text{cov}_{YY})}$, where cov_{XY} is the cross-covariance obtained from both the value of mothers for trait X on the mean value of daughters for trait Y and the value of mothers for trait Y on the mean value of daughters for trait X . Cov_{XX} and cov_{YY} are the covariances of the value of mothers on the mean value of daughters for each trait (Falconner & Mackay, 1996). Standard errors associated with genetic correlations were estimated as $(1 - r_a^2/\sqrt{2})[\text{se}(h_x^2)\text{se}(h_y^2)/h_x^2 h_y^2]^{1/2}$ following Falconner & Mckay (1996).

Variance and covariance components were also estimated with an animal model by Derivative Free Restricted Maximum Likelihood (DFREML 3.0; Meyer, 1989, 1997). The Maximum Likelihood method is particularly suitable for quantitative genetic analyses based on pedigree data with unequal family size (Shaw, 1987;

Table 1 Data available for DFREML univariate analyses on maternal traits of bighorn ewes in the Ram Mountain population 1973–1998. Absolute maternal expenditure is lamb mass adjusted to 15 September. Relative maternal expenditure is the ratio of lamb mass on ewe mass, both adjusted to 15 September.

Data structure	No. of individuals
N records	303
N animals	128
Base animals	36
Animals with records	117
Dams with progeny records	61
Grand dams with progeny records	30
Traits	Mean \pm SD
Body mass	69.57 \pm 4.92
Absolute maternal expenditure	26.51 \pm 0.80
Relative maternal expenditure (arcsine)	0.67 \pm 0.03

Cheverud & Dittus, 1992). Sires were coded '0' in pedigrees and the convergence criterion was set to 10^{-8} . Between 1 and 10 reproductive records were available for each ewe. To estimate maternal traits, we first fitted univariate models:

$$y = Xb + Z_1a + Z_2p + e$$

where y is the trait record; b and a are the vectors of fixed and random additive effects, and p is the vector of individual permanent environmental effects; X , Z_1 and Z_2 are the corresponding incidence matrices relating the effects to y ; e is the vector of residuals. The structure of the data is reported in Table 1. We built 2 models; Model 1 included a permanent environmental effect, and Model 2 excluded it. Likelihood ratio tests were used to select the model with the best fit. The difference in likelihood function ($-2[\log \text{likelihood Model 1} - \log \text{likelihood Model 2}]$) was assumed to have a χ^2 distribution with degrees of freedom equal to the difference in number of parameters between the two models (here d.f. = 1). Approximate sampling errors were given by the program by the quadratic approximation of the likelihood (Meyer, 1989). Additive covariances and genetic correlations between ewe mass and maternal expenditure indices (absolute and relative) were estimated by bivariate analyses using DFREML 3.0 (Meyer, 1989, 1997). Coefficients of additive genetic and residual variation were calculated following Houle (1992).

Female size and adjustment of maternal expenditure

Because the fitness costs of reproduction are greater for small than for large females (Festa-Bianchet *et al.*, 1998), and because maternal expenditure decreases with increasing population density (Festa-Bianchet & Jorgenson, 1998), we expected that as density increased, small females would decrease maternal expenditure more rapidly than large females. To test this hypothesis at the individual level, we estimated for each ewe the slope of

the regression between absolute maternal expenditure and density. We then used that slope as an index of individual adjustment of maternal expenditure to changes in density. Absolute maternal expenditure was standardized by lamb sex because we did not have enough data to adjust maternal expenditure for each sex separately. A negative slope would indicate a decrease in absolute maternal expenditure with increasing density. Only ewes that experienced changes in density of more than 15 ewes between reproductive episodes were considered. Individual ewes experienced different population densities during their lifetime, and because most density-dependent changes in population dynamics were nonlinear (Jorgenson *et al.*, 1993; Portier *et al.*, 1998), we expected that the strength of the adjustment in maternal expenditure would depend on the maximum population density experienced by each ewe. We therefore divided the data set in three groups according to population density: (1) first and last lambs born at low density; (2) first lamb born at low density and last lamb born at high density; (3) first and last lambs born at high density, where years with <75 females were considered low density and years with >75 females were considered high density. An ANCOVA was performed on maternal adjustment with ewe size as a covariate (see above) and density as a factor.

Results

Festa-Bianchet & Jorgenson (1998) found a cubic polynomial relationship between lamb and ewe mass using unstandardized data. With standardized mass and two more years of data, linear regression provided the best fit to the relationship between lamb and ewe mass ($F_{1,347} = 18.892$, $P < 0.001$). Ewe mass, however, explained less than 5% of the variation in lamb mass, as reported by Festa-Bianchet & Jorgenson (1998). The slope of the regression was 0.04: as ewe mass increased by 33% from 60 to 80 kg, predicted lamb mass only increased by 3%, from 26.4 to 27.2 kg. The average (\pm SE) relative maternal expenditure was 0.38 ± 0.002 (based on each female's average ratio of lamb on ewe masses; untransformed data; $n = 145$ females).

Quantitative genetics

Heritability estimates based on the mean daughters/mother regression method were all high and significantly different from zero (Table 2). The phenotypic and the genetic correlations between body mass and absolute maternal expenditure were both positive and moderate, although only the phenotypic correlation was significantly different from zero. A positive phenotypic correlation and no genetic correlation were found between absolute and relative maternal expenditure. Body mass and relative maternal expenditure had strong negative genetic and phenotypic correlations.

Table 2 Heritability (h^2 : diagonal), phenotypic correlations (r_p = below diagonal) and genetic correlations (r_a = above diagonal) of ewe mass and maternal expenditure for the Ram Mountain bighorn sheep population, estimated with the mother–daughter regression method. Absolute maternal expenditure was measured by lamb mass adjusted to 15 September. Relative maternal expenditure was the ratio of lamb mass on ewe mass, both adjusted to 15 September. Standard errors of heritability estimates were twice those of the regression coefficient. Standard errors of r_a were estimated following Falconner & Mackay (1996). Number of families was 65 ($F_{size} = 1.43$) for ewe body mass, 60 ($F_{size} = 1.36$) for absolute maternal expenditure and 56 ($F_{size} = 1.36$) for relative maternal expenditure. Estimates significantly different from zero at $\alpha = 5\%$ are indicated in bold type.

	Body mass	Absolute maternal expenditure	Relative maternal expenditure
Body mass	0.42 ± 0.20	0.33 ± 0.29	-0.99 ± 0.01
Absolute maternal expenditure	0.23 ± 0.08	0.41 ± 0.22	-0.04 ± 0.36
Relative maternal expenditure	-0.91 ± 0.09	0.14 ± 0.09	0.56 ± 0.22

REML estimates of variance/covariance components, heritability, phenotypic and genetic correlations, of ewe mass and maternal expenditure indices are shown in Table 3. When repeated measures from the same individual are available, the REML procedure allows us to estimate permanent environmental effects that are due to characteristics proper to a specific individual. Removing permanent environmental effects did not decrease the likelihood of univariate models for heritability of ewe mass (difference in $\log L = 0.425$; $P > 0.05$), absolute maternal expenditure (difference in $\log L = 0.0001$), and relative maternal expenditure (difference in $\log L = 0.179$; $P > 0.05$). Therefore, a model without permanent environmental effects was selected for all traits. Heritability and genetic correlations based on REML were very similar to the estimates obtained with the daughters/mother regression (Table 3B), except for absolute maternal expenditure for which REML pro-

duced a lower estimate. Additive genetic and residual coefficients of variation based on REML estimates were all low (body mass: $CV_a = 5.47$; $CV_r = 4.35$; absolute maternal expenditure: $CV_a = 1.12$; $CV_r = 2.76$; relative maternal expenditure: $CV_a = 3.13$; $CV_r = 2.87$).

Ewe mass and adjustment of maternal expenditure to changes in density

More than 70% of females ($N = 55$) weaned smaller lambs as density increased (Fig. 1). A model with ewe mass, population density and their interaction explained about 40% of the variance in maternal expenditure adjustment ($R^2 = 0.38$; $F_{5,49} = 5.985$; $P = 0.0002$). Individual ewes were more likely to adjust lamb weaning mass to variations in density as the peak population density that they experienced increased ($F_{2,49} = 7.477$; $P = 0.002$). The adjustment of lamb weaning mass to density was stronger for smaller than for larger ewes ($F_{1,49} = 5.783$; $P = 0.02$). Finally, we found a significant interaction effect: the relationship between female body mass and adjustment increased with the maximum density experienced by individual ewes ($F_{2,49} = 6.896$; $P = 0.002$).

Discussion

Our results revealed additive genetic effects on phenotypic variation in ewe body mass and in both absolute and relative levels of maternal expenditure. Adult ewe mass and relative maternal expenditure were highly heritable. The low but significant heritability of lamb weaning mass, as a maternal trait, suggests that the daughters of ewes that wean large lambs also tend to wean large lambs. There is therefore a potential for the evolution of these traits in the population (Roff, 1997; Lynch & Walsh, 1998). We previously estimated the heritability of weaning mass as an individual trait (comparing a ewe's mass as a lamb with the mean mass

Table 3 REML estimates of quantitative genetic parameters of ewe mass and maternal expenditure for the Ram Mountain bighorn sheep population, Alberta. Absolute maternal expenditure is measured by lamb mass adjusted to 15 September. Relative maternal expenditure is the ratio of lamb mass on ewe mass, both adjusted to 15 September. **A:** Variance/covariance components: V_a (V_p ; between parentheses) (diagonals); Cov_a (above diagonals); Cov_p (below diagonals). **B:** h^2 estimates (diagonals), and r_a (above), and their standard errors. Estimates significantly different from zero at $\alpha = 5\%$ are shown in bold type.

	Body mass	Absolute maternal expenditure	Relative maternal expenditure
A			
Body mass	14.472 (23.642)	0.298	-0.074
Absolute maternal expenditure	0.519	0.088 (0.624)	0.270 10^{-3}
Relative maternal expenditure	-0.074	0.296 $\times 10^{-3}$	0.44 $\times 10^{-3}$ (0.81 $\times 10^{-3}$)
B			
Body mass	0.61 ± 0.06	0.26 ± 0.35	-0.99 ± 0.08
Absolute maternal expenditure		0.14 ± 0.07	0.05*
Relative maternal expenditure			0.54 ± 0.06

*Sampling error could not be estimated, probably because of the weakness in the log-likelihood function.

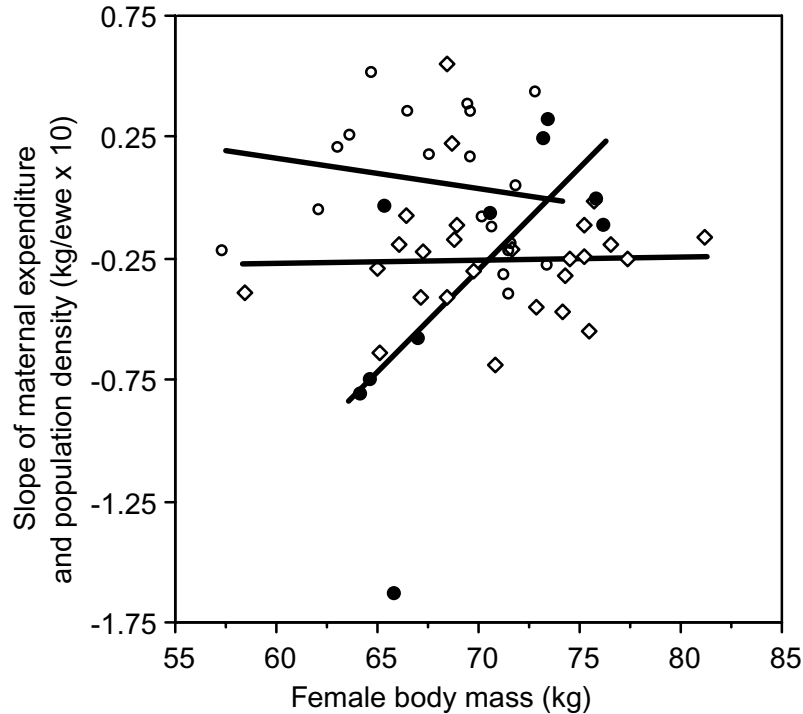


Fig. 1 Changes in the slope of the relationship between population density and absolute maternal expenditure according to ewe body mass in the Ram Mountain population 1973–98. Diamonds = ewes that produced lambs only in years with less than 75 adult ewes in the population; open circles = ewes that produce lambs in years with more and with less than 75 ewes; filled circles = ewes that produce lambs only in years with more than 75 ewes.

of her lambs), and found it to be moderate with the REML method (0.29 ± 0.13) and low with the offspring–mother regression method (0.02 ± 0.18) (Réale *et al.*, 1999). Because the heritability of body mass increased with age, we hypothesized that the low heritability estimate of body mass early in life was a consequence of strong negative maternal effects for lambs and yearlings (Réale *et al.*, 1999). As a result, mass-related differences in maternal expenditure among ewes may decrease the phenotypic variation of lamb mass at weaning.

Although variation in propagule size is generally assumed to depend mostly on maternal genetic or phenotypic characteristics, some of that variation may be affected by other factors (Weigensberg *et al.*, 1998). Lamb weaning mass can be a maternal trait but is also an individual trait of the lamb, and could be affected by the direct additive genetic influences of mothers and fathers. Bighorn sheep have a promiscuous mating system: often several rams copulate with an oestrus ewe, and paternity is determined by sperm competition (Hogg & Forbes, 1997), suggesting little assortative mating. It is therefore possible that some of the variation in mass between siblings could be due to genetic differences among fathers. Alternatively, genetic differences in metabolic efficiency and summer growth rate for lambs of ewes of

different size may explain the small variation in weaning mass between lambs of small and large ewes. That explanation implies that small individuals will have a high metabolic efficiency as lambs and a low efficiency as adults, but genetic correlations of the same trait at different ages are generally positive (Cheverud *et al.*, 1983). Finally, lamb growth can be affected by non-genetic traits such as disease (L'Heureux *et al.*, 1996), weather and forage availability because lambs begin to forage on vegetation well before weaning (Festa-Bianchet, 1988). Festa-Bianchet & Jorgenson (1998), however, have shown that the density-dependent decrease in weaning mass can be attributed to a decrease in maternal expenditure rather than to a decrease in forage intake. Our analyses limited environmental effects by standardizing weaning mass according to population density and climate.

Because ewe mass was weakly correlated to absolute maternal expenditure, while ewe mass and relative maternal expenditure were highly heritable and strongly negatively correlated, our results suggest a size-dependent negative maternal effect. We propose that small ewes produce genetically small lambs but then provide more care than large ewes, leading to a very weak heritability of lamb weaning mass as a maternal trait, to

a very weak relationship between ewe mass and lamb weaning mass, but also to strong heritabilities of both adult mass and relative maternal expenditure. Large ewes should have daughters with low relative maternal expenditure and small ewes should have daughters with high relative maternal expenditure. Since genetically correlated traits cannot evolve independently (Price & Langen, 1992), a selective pressure for increased adult mass could lead to a decrease in relative maternal expenditure without strongly affecting offspring weaning mass.

Our results support the hypothesis of a co-adaptation of maternal and offspring traits caused by selection on offspring size (Wolf & Brodie, 1998). A size-dependent maternal expenditure strategy may have evolved because of the relationship between weaning mass and fitness. Lamb winter survival increases with weaning mass, particularly at high density (Festa-Bianchet *et al.*, 1997), but is independent of maternal mass (Festa-Bianchet *et al.*, 1998), probably because size-dependent maternal expenditure leads to a weak relationship of maternal mass and weaning mass. If offspring fitness did not increase linearly with weaning mass, large ewes that produced genetically large lambs may not be selected to devote a high proportion of their resources to their lamb, if the additional maternal expenditure had a weak impact on offspring fitness while inducing fitness costs to the mother. Stabilizing selection on birth mass, reported for other mammals (Schluter & Nychka, 1994), or physical constraints during gestation (Roff, 1992) may lead to an upper limit of birth mass and constrain the variability of lamb mass at weaning. An overriding effect of selection on birth mass, however,

could not explain why, as population density increased, small females decreased maternal expenditure more than large ewes.

If small ewes used a higher proportion of available resources for maternal expenditure compared to large ewes, the maternal expenditure of small ewes should be constrained to a higher extent than that of large ewes by density-dependent resource limitation. Confirming this prediction, as population density increased, small ewes experienced a greater decrease in reproductive success and a greater increase in costs of reproduction compared to large ewes (Festa-Bianchet *et al.*, 1998). Ewes curtail reproductive expenditure when resources are scarce (Festa-Bianchet & Jorgenson, 1998) and favour their own residual reproductive value over their lamb's survival. The constraints on reproductive strategy imposed by variation in resource availability appear to differ according to ewe mass, because maternal expenditure was more sensitive to increasing density for small than for large ewes. Maternal expenditure strategies of bighorn ewes show a high degree of phenotypic plasticity associated with body mass, as one may expect in a species where individuals can experience high variability in intraspecific competition over their lifetime (Festa-Bianchet *et al.*, 1998).

Based on the limited data available for large mammals (Table 4), bighorn sheep, and probably ovids in general, seem to be characterized by a weak correlation of offspring and maternal mass. Although a positive correlation between offspring and maternal mass was found in all cases, only one study demonstrated that maternal expenditure was constant relative to maternal

Table 4 Relationships between offspring mass and maternal mass within populations of large mammals.

Species	Common name	Age*	Relation†	Equation	r or proportion of variance explained	Reference
<i>Ovis canadensis</i>	Bighorn sheep	June‡	+(<1)	$y = 5.028 + 0.07x$	0.21	Festa-Bianchet, unpublished data
<i>Ovis canadensis</i>	Bighorn sheep	weaning	+(<1)	$y = 23.89 + 0.04x$	0.22	This study
<i>Ovis aries</i>	Soay sheep	birth	+	multiple regression	7.1%	Clutton-Brock <i>et al.</i> (1996)
<i>Dama dama</i>	Fallow deer	birth	+	$y = 1.77 + 0.07x$	0.61	Birgersson & Ekvall (1997)
<i>Dama dama</i>	Fallow deer	prewinter	+	$y = 16.9 + 0.21x_1$	0.43	Birgersson & Ekvall (1997)
<i>Rangifer tarandus</i>	Reindeer	weaning	+	$y = 7.36 + 0.51x_1 + 22.38x_2$	0.63 (partial r)	Kojola (1993)
<i>Ursus maritimus</i>	Polar bear	spring cub	+	?	0.45/0.40/0.13¶	Derocher & Stirling (1997)
<i>Ursus maritimus</i>	Polar bear	autumn cub	+	?	0.64/0.67/0.69¶	Derocher & Stirling (1997)
<i>Mirounga leonina</i>	Elephant seal	birth	+(<1)	$\log y = 0.64 + 0.50 \log x$	0.62	Amborn <i>et al.</i> (1997)
<i>Mirounga leonina</i>	Elephant seal	weaning	+(<1)	$\log y = 0.05 + 0.76 \log x$	0.79	Amborn <i>et al.</i> (1997)
<i>Halichoerus grypus</i>	Grey seal	birth	+(<1)	$\log y = 0.99 + 0.34 \log x$	0.32	Pomeroy <i>et al.</i> (1999)
<i>Halichoerus grypus</i>	Grey seal	weaning	+ (=1)	$\log y = -0.56 + 0.82 \log x$	0.36	Pomeroy <i>et al.</i> (1999)
<i>Phoca vitulina</i>	Harbor seal	birth	+	?	0.42/0.32	Bowen <i>et al.</i> (1994)

*Time when mass was measured. †Relationship between mass of the offspring and that of its mother: – significantly negative; 0 = not different from zero; + = significantly positive. Between parentheses: slope is significantly different from 1 or not. ‡Mass in June: lamb mass adjusted to 15 June; ewe mass adjusted to 12 June. Most lambs are about 3 weeks old at this time. Data were not adjusted for population density. §Regression for females is shown, but there was no difference between male and female offspring. ¶Average for male and female cubs; 1, 2 and 3 cubs per litter, respectively.

mass (regression slope = 1). For polytocous mammals, the relationship between litter mass and mother mass is likely to be stronger than the relationship between individual offspring mass and maternal mass reported in Table 4 because both litter size and individual offspring mass may vary. We therefore hypothesized that both the phenotypic and the genetic relationships between relative maternal expenditure and maternal mass will rarely be positive. The mass-dependent reproductive strategies we found in bighorn sheep may also occur in other mammals, although they may be weaker in other species if indeed the correlation of offspring and maternal mass in ovids is weaker than in other mammals (Table 4). Both quantitative genetic models (Wolf & Brodie, 1998) and empirical analyses (reviewed by Cheverud & Moore, 1994; Roff, 1997) have shown that the direct-maternal genetic correlation is generally negative.

What are the possible evolutionary causes and consequences of a negative correlation of relative maternal expenditure and maternal mass? For juveniles, body mass is often positively related to survival (Festa-Bianchet *et al.*, 1997). As suggested by our results, negative maternal effects (i.e. the relatively higher maternal expenditure of small females compared to large ones) may allow small females to produce viable offspring while preventing large females from incurring high costs of reproduction. Thus, size-dependent reproductive strategies may exist in other species, and selection on juvenile mass may have shaped the relationship between maternal mass and reproductive expenditure in most species. Maternal effects on body size should decrease with offspring age (Cheverud, 1984; Rossiter, 1996), possibly explaining why sheep in the study population exhibit considerable variation in adult mass despite results that consistently suggest a selective advantage of large mass (Festa-Bianchet *et al.*, 1998; Bérubé *et al.*, 1999). As suggested by Bernardo (1996), maternal effects may thus affect population parameters. Studies on other species are needed to investigate the prevalence of mass-dependent reproductive strategies in mammals. Heritable mass-dependent maternal expenditure may be considered as a maternal effect that affects variation in individual phenotypes, and may have important consequences for the evolution of body mass and life history traits.

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