Mass- and Density-Dependent Reproductive Success and Reproductive Costs in a Capital Breeder

Marco Festa-Bianchet,[1,2,*] Jean-Michel Gaillard,[2,†] and Jon T. Jorgenson[3,‡]

1. Groupe de recherche en écologie, nutrition, et énergétique, Département de biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada;
2. UMR 5558, Laboratoire de Biométrie-Génétique et Biologie des Populations, Université Claude-Bernard Lyon 1, 69622 Villeurbanne Cedex, France;
3. Alberta Department of Environmental Protection, Natural Resources Service, Canmore, Alberta T1W 1P1, Canada

ABSTRACT: For capital breeders, mass may affect reproductive potential. Reproductive expenditure may reduce future reproductive potential, particularly when resources are scarce. To test the hypothesis that reproductive success and the costs of reproduction vary according to mass and population density, we analyzed 25 yr of data on bighorn ewes (*Ovis canadensis*). The number of adult females was first limited by yearly removals, then allowed to triple. We found no survival costs of reproduction for ewes aged 4–7 yr. For ewes aged 8–14 yr, survival was density dependent for barren ewes but not for ewes that weaned lambs. Failure to lamb was rare and negatively correlated with fertility the following year. At low population density, lactation had a negative effect on mass gain but had a limited reproductive cost. At high density, heavy ewes had higher reproductive success than light ewes, and the reproductive cost and somatic costs of reproduction increased. The cost of reproduction was greater for light than for heavy ewes. Survival of weaned lambs to 1 yr was affected by population density but not by maternal mass or previous reproductive success. In large mammals, manipulations of reproductive effort are problematic, but long-term monitoring of individual mass and reproductive success under varying conditions of resource availability can provide insights into the evolution of life histories.

Keywords: reproductive costs, phenotypic correlations, capital breeders, body mass, reproductive potential, life history.

* E-mail: mbianche@courrier.usherb.ca.

† E-mail: gaillard@biomserv.univ-lyon1.fr.

‡ E-mail: jjorgens@env.gov.ab.ca.

The notion of a fitness cost of reproduction is fundamental in theories of life-history evolution, but disagreement exists over how this cost should be measured. Phenotypic correlations, which compare the reproductive histories of different individuals to determine whether components of reproductive success are negatively correlated, are often considered unreliable because of individual heterogeneity in reproductive potential (Reznick 1985, 1992; van Noordwijk and de Jong 1986; Partridge and Harvey 1988). Experimental manipulations of reproductive effort or selection experiments have been recommended to study reproductive costs, but these methods are not problem free (Partridge 1992). Several observational studies of reproductive costs in mammals have not found trade-offs between fitness components (Murie and Dobson 1987; Festa-Bianchet 1989; Festa-Bianchet and King 1991; Millar et al. 1992; Byers 1997), likely because of differences in individual reproductive potential. However, other observational studies have revealed negative phenotypic correlations between components of reproductive success in large mammals (Clutton-Brock et al. 1983; Berger 1989; Green and Rothstein 1991; Sydeman et al. 1991; Hogg et al. 1992; Kojola and Helle 1993; Marrow et al. 1996). Large mammals are considered "capital breeders," because they are thought to rely partly on accumulated body reserves to satisfy the energy needs of reproduction, in contrast to "income" breeders that meet those same energy needs by relying almost entirely on short-term food acquisition (Stearns 1992; Jönsson 1997). If large mammals are capital breeders, when resources are limited, reproductive effort should affect body reserves and subsequent ability to reproduce. Therefore, for capital breeders under resource limitation, phenotypic correlations could provide a useful assessment of the costs of reproduction if individual differences were accounted for by an independent measure of reproductive potential, such as body mass.

Because of viviparity and of highly developed offspring recognition mechanisms, manipulations of reproductive effort in wild mammals are difficult and have been

mostly limited to rodents that give birth to altricial young in nests or burrows (Hare and Murie 1992; Humphries and Boutin 1996). Partridge (1992) pointed out that genetic methods to measure reproductive costs are limited to the narrow taxonomic range of species amenable to such experiments. Experimental manipulations of reproductive effort suffer from a similar limitation: they have become routine for birds or insects but are difficult for mammals, particularly for those that are capital breeders. Because the life-history strategies of capital and income breeders may be fundamentally different (Jönsson 1997), restricting investigations of reproductive costs to a narrow range of taxonomic groups that are mostly income breeders would limit the development of life-history theory. While experimental manipulations of reproduction are clearly desirable, we suggest that statistical control of individual characters that may affect reproductive success is a valid method to measure reproductive costs. A promising yet unexplored approach to assessing the costs of reproduction in wild mammals is to account for individual differences in reproductive potential by including individual body mass in the analysis of reproductive costs. If mass is a measure of individual quality, its statistical control could provide an alternative to experimental manipulations in the investigation of the fitness costs of reproduction. Our goal here is not to measure evolutionary trade-offs among different sets of genotypes but rather to quantify the survival and future fecundity costs of current reproduction (Reznick 1992).

Few studies have measured the body mass of large mammals of known reproductive history, and little is known about how mass affects reproductive success or how reproduction affects mass. In capital breeders, large individuals may reproduce more successfully and with a lower fitness cost than small individuals, particularly in species with little or no variability in litter size, such as many ungulates (Carranza 1996). In American bison (*Bison bison*), Green and Rothstein (1991) found that heavy juvenile females matured earlier but were smaller as adults than light juvenile females. In contrast, for bighorn sheep (*Ovis canadensis*), early primiparity affected mass gain only at high population density (Festa-Bianchet et al. 1995). In bison, adult mass was negatively related to reproductive success because nonreproductive females were the largest and the heaviest. The direction of causality between mass and reproductive success is therefore unclear: large individuals could have greater reproductive success than small individuals, but limiting reproductive expenditure could lead to large size.

Interspecific differences in body mass have a major effect on the reproductive biology of mammals. In general,

as body mass increases, yearly reproductive rate decreases (Peters 1983; Calder 1984). The opposite pattern may occur intraspecifically: large females can have higher seasonal reproductive success than small females (Sæther and Haagenrud 1983; Green and Rothstein 1991; Reiter and LeBoeuf 1991; Cameron et al. 1993; Wauters and Dhondt 1995). In particular, female mass is often associated with age of primiparity (Reimers 1983; Green and Rothstein 1991; Gaillard et al. 1992; Jorgenson et al. 1993a) and litter size (Michener 1989; King et al. 1991; Campbell and Slade 1995; Hewison 1996). However, the relationships between mass and reproduction are often weak, and some studies report no effect of mass on reproductive success (Hansson 1992; Millar et al. 1992; Morris 1996b). Possibly, large individuals may only obtain a reproductive advantage over smaller ones when resources are scarce. If that was the case, only long-term studies that monitored individuals under a wide range of environmental conditions could assess the effects of individual mass on reproductive success.

The relationships between body mass, population density, and reproductive performance are of interest because life-history theories predict a trade-off between mass and reproduction when resources are limited (Stearns 1992). Recent theories of state-dependent reproductive strategies (Marrow et al. 1996; McNamara and Houston 1996; Morris 1996a) predict that individual reproductive effort is condition dependent and should vary according to the condition-specific risks posed by environmental variation. Empirical tests of these theories are rare because they require long-term data on individual reproductive success and body mass under varying levels of resource availability, as well as an evaluation of how different levels of reproductive expenditure may affect subsequent survival and reproductive success. In feral sheep undergoing cyclic density changes, mass had a positive effect on adult ewe survival, particularly in years of peak density that led to high mortality (Clutton-Brock et al. 1996). Reproductive effort, however, did not affect ewe survival or subsequent reproduction (Clutton-Brock et al. 1997).

Here we use long-term data on a large mammal to test the hypothesis that, in capital breeders, reproduction involves costs in terms of survival, subsequent reproductive success, and changes in body mass and that these costs vary with population density and female mass. We expected that heavier females would have greater reproductive success and lower fitness costs of reproduction than lighter females and that the costs of reproduction would be most evident at high population density. To test these predictions, we compared individual mass and reproductive success of bighorn ewes from a 25-yr study where we

obtained accurate information on mass and reproduction of marked females.

Methods

Study Area and Population

Bighorn sheep have been monitored at Ram Mountain (52°N 115°W, elevation 1,082–2,173 m), Alberta, Canada, since 1971. Data used in this article were collected in 1973–1997. From late May to early October, sheep were captured in a corral trap baited with salt and weighed to the nearest 250 g with a Detecto spring scale (Brooklyn, N.Y.). Ewes were individually marked with canvas collars; 100% of ewes were marked from 1976 onward. Ewe reproductive status was determined by udder examination at capture and by observing lambs suckle. Lambs were marked with numbered Ketchum metal tags (Ketchum Manufacturing, Ottawa, Ontario) in both ears and a small strip of colored Safeflag plastic (Pawtucket, R.I.).

From 1972 to 1981, we limited the population at 30–33 adult ewes through yearly ewe removals (Jorgenson et al. 1993b). After 1981, the population increased, peaked at 104 ewes in 1992, and declined to 75 ewes by 1997.

Definition of Yearly Reproductive Success Categories

We classified ewes into several categories that reflected increased energy expenditure for gestation and lactation. Ewes were considered "barren" in years when they did not show any evidence of lactation. Ewes whose lamb died before October were included in a category of "summer loss." In 64% of these cases, the lamb died at or soon after birth: the ewe showed evidence of lactation when captured in late May or early June, but no lamb was seen. "Summer loss" ewes expended little or no energy in lactation. Ewes whose lamb died between October and May were included in a category of "winter loss." Only ewes whose marked lamb had been identified as their offspring could be in this category because, by the following May, almost all lambs no longer associated with their mothers.

For analyses where we considered the effects of raising a lamb to 1 yr of age, the reproductive success of ewes whose lamb survived to October but may or may not have survived to 1 yr was considered "unknown." This group included cases when the lamb was unmarked or the mother was not identified. Survival of the lamb to 1 yr was measured by sighting the lamb in late May or early June the year following birth.

Finally, for some analyses, we were interested in assessing the consequences of complete lactation. All ewes whose marked or unmarked lamb survived to October, were assumed to have "weaned a lamb." This group therefore included ewes in the winter loss, survival to 1 yr, and unknown categories.

Data Analysis

We adjusted individual mass to September 15 using each ewe's own rate of mass gain, determined by repeated weighings each summer as described elsewhere (Festa-Bianchet et al. 1996). By mid-September, ewes have nearly ended their summer mass accumulation (Festa-Bianchet et al. 1996); therefore mass adjusted to September 15 approximates mass at the beginning of the winter season, during which ewes lose mass.

Our analyses involved 142 ewes aged 4–14 yr. Most 2-yr-old ewes do not produce lambs (Jorgenson et al. 1993a), and at high density, most 3-yr-old ewes also failed to reproduce (M. Festa-Bianchet, J.-M. Gaillard, and J. T. Jorgenson, unpublished data). In addition, ewes aged 2 and 3 yr are considerably lighter than older ewes (Festa-Bianchet et al. 1996). We therefore excluded 2-yr-old and 3-yr-old ewes from our analyses. We also excluded ewes older than 14 yr because very old ewes lose mass as they age, they show reproductive senescence (Bérubé 1997), and few were present at low population density.

We used three levels of population density: ewes that were born and reproduced at low density, ewes born at low density that reproduced at high density, and ewes that were born and reproduced at high density. We considered years up to and including 1987 as low density (average of 40 ewes and 120 total sheep in June), while 1988–1997 (average of 84 ewes and 196 total sheep) were considered high-density years. Ewes born at low density could reproduce within two classes of density: for example, a ewe born in 1982 would receive a density code of 1 in 1986 and 2 in 1990. Our analyses therefore took into account the possibility that population density during early development and in the year of reproduction may have different effects on reproduction (Langvatn et al. 1996).

Our statistical analysis followed three steps. First, we used logistic models to test whether reproductive success (three modalities: barren, summer loss, and weaned a lamb) affected ewe survival. To account for the possible effects of ewe age, change in mass from a year earlier, and population density (three modalities as explained above) on the relationship between reproductive success and ewe survival, we used a three-way ANCOVA-like procedure, which included tests for differences in slopes and in intercepts of the logistic regression of ewe survival

(a variable with a binomial error distribution) on changes in mass according to ewe age, population density, and previous reproductive success. To account for the unbalanced sampling design (different sample sizes in different modalities), we used a backward procedure to select the final model (Searle 1971). Thus, we first fitted the most general model (different logistic regressions of ewe survival on changes in mass according to each combination of age, density, and previous reproductive success). Following Schemper (1990), we calculated the proportion of explained variation of this general model as (dev 1 − dev 2)/dev 1, where dev 1 is the deviance of the null model (constant ewe survival) and dev 2 is the deviance of the general model. We then withdrew from the model the effect of the four-way interaction (the effect of the three-way interaction of age, density, and reproductive success on the slope of the logistic regression of ewe survival on changes in mass). We tested this effect with a likelihood-ratio test that compares the difference in deviance between two nested models, which is distributed as a χ^2 statistic with a number of degrees of freedom equal to the difference in the number of parameters in the two models. If the four-way interaction did not have a significant effect, we tested the four terms of the three-way interactions (the effects of the two-way interactions of reproductive success and age, reproductive success and density, age and density, as well as the effects of the three-way interaction of reproductive success, age, and density on the intercept) by successively withdrawing each of these terms. The effect of a given term was always tested by accounting for the effects of all the other terms for a given level of analysis, whether the other terms were significant or not. If no term of the three-way analysis had a significant effect, we tested for the six terms of the two-way level of analysis (the main effects of reproductive success, density, and age on the slope of the logistic regressions and the two-way interaction of reproductive success and age, reproductive success and density, and age and density on the intercept) by successively withdrawing each of these terms. Finally, if no two-way interaction was significant, we tested for the main effects of the factors (density, reproductive success, and age) and of the covariable (change in mass). When either the four-way interaction or one of the four three-way interactions was significant, we replicated the analysis at each of the modalities of the factor most involved in the interaction to avoid complex higher-order interactions that are difficult to interpret.

In a second step, we analyzed the effects of ewe mass on September 15 on reproductive success the following year with a series of logistic regressions. We first considered all ewes and determined whether fertility was affected by density, reproductive success the previous year, and mass. We then excluded barren ewes and looked at the probability of lamb survival to weaning. Finally, we excluded ewes in the barren, summer loss, and unknown categories and analyzed the probability of rearing a lamb to 1 yr of age for ewes whose lambs survived to weaning. With the same ANCOVA-like procedure described above, we included in the logistic regressions the effects of density and reproductive success the previous year. We did not distinguish between ewes whose lambs did or did not survive the winter because a preliminary analysis where these two categories of previous reproductive success were kept separated did not reveal any differences in their effects on subsequent reproduction.

Using the selected models for each level of reproductive success, we then tested for a potential effect of ewe age (although none was expected, see Bérubé 1997) by adding the main effect of age on the intercepts of the logistic regressions and on the slopes of the logistic regressions to the selected model for each level of reproductive success. Finally, to examine whether individual differences affected our results, we considered only ewes that were sampled for a minimum of 5 yr, which left us with 41 ewes for examining fertility, 32 ewes for weaning success, and 13 ewes for lamb survival to 1 yr. We first tested whether each selected model from the overall analysis of each level of reproductive success was significant for the reduced subsamples and then tested for the presence of an individual-ewe effect by adding ewe identity to the selected model. The survival of ewes decreases after age 7 yr (Jorgenson et al. 1997), and for the individual-level analyses, we used two age classes, 4–7 yr and 8–14 yr, because each ewe was necessarily only sampled once within any 1-yr class.

In a third step, we examined whether a ewe's change in body mass from September 15 in year $t - 1$ to September 15 in year t was affected by her reproductive success in year t (barren, summer loss, or weaned a lamb), her age, and population density. We used a three-way ANOVA and tested for all possible interactions among factors. As in the first and second steps, we accounted for the unbalanced sampling design of our analysis by first fitting the most general model (with a three-way interaction of reproductive success, age, and density). We then tested for the three-way interaction by comparing the general model with a model including only the two-way interactions (reproductive success and age, reproductive success and density, age and density) using an *F*-test. When the three-way interaction was not significant, we withdrew each of the two-way interactions successively to test each one while accounting for all the others. Last, when no two-way interaction was significant, we tested for the main effects of reproductive success, age, and density on the ewe's changes in mass by withdrawing

successively each of these factors. As in the previous analyses, the effect of one factor was always tested while accounting for the effects of all other factors. To examine individual effects, we considered 43 ewes for which we had at least 5 yr of data. We first tested whether the model selected from the overall analysis of changes in mass was significant for the reduced subsample and then tested for the presence of an individual-ewe effect by adding ewe identity to the selected model. We also checked again for a possible age effect by adding two age classes (4–7 yr and 8–14 yr) to the selected model.

Before performing our analyses, we checked for potential problems of collinearity. We found that most correlations among independent variables were weak and not significant. For female survival, the strongest correlation (0.40) was between level of reproductive success and change in mass; all the others were less than 0.25. For the analyses of reproductive success and of costs of reproduction, the strongest correlation was between ewe age and mass (0.39) followed by that between reproductive success and density (0.27); all others were less than 0.17.

Analyses that did not include an individual effect were affected to an unknown extent by pseudoreplication (Machlis et al. 1985), but no individual ewe contributed more than 1.4% of any data set. Lamb sex, reproductive success, population density, mass, and age varied over the life span of each individual, decreasing the potential dependence of data points. If each ewe had a strong tendency to return to the same mass in consecutive years, our analyses would suffer from autocorrelation. To assess the extent of autocorrelation, we compared mass adjusted to September 15 to mass 1 yr earlier. Less than half of the variability in mid-September mass was explained by the ewe's mass 1 yr earlier ($N = 482$ ewe-years; mass $= 26.6 + 0.64$[mass 1 yr earlier], $r^2 = 0.46$, $P < .001$).

Statistical analyses were performed using GLIM (Francis et al. 1993). Means are reported ± 1 SD and all probabilities are two tailed unless otherwise indicated. In reporting our results, we have simplified the technical and statistical content of the text in order to summarize the biological implication of our analyses. We present statistical details in the tables, including the steps followed in model selection.

Results

Ewe Survival

There were no survival costs of reproduction, regardless of differences in ewe age or body mass (table 1). When we considered all ewes, we found several complex three-way interactions, all involving age. Therefore, we repeated the analysis for ewes aged 4–7 and 8–14 yr. For the younger age class, survival was independent of repro-

ductive success, population density, and change in mass from the previous year (table 1).

For ewes aged 8–14 yr, we found a significant interaction of reproductive success and density (table 1), suggesting a negative effect of density on survival that decreased with increasing reproductive success. For barren ewes, our model's estimates of annual survival were 0.67, 0.50, and 0.00 at the three levels of density considered in our analysis, while, for ewes whose lambs survived the winter, survival did not decrease with increasing density: annual estimates were 0.89, 0.88, and 1.00 at the three levels of density.

Effects of Mass, Population Density, and Previous Reproduction on Reproductive Success

Fertility. It was rare for adult ewes not to reproduce: we found no evidence of lactation for only 9.6% of ewe-years included in our sample, and fertility did not vary according to age (table 2; $N = 553$ ewe-years). However, 50% of ewes were barren at least once while aged 4–14 yr. The relationship between ewe mass and fertility did not vary according to either population density or reproductive success the previous year (table 2). There was no evidence of a reproductive cost of fertility: on the contrary, fertility was higher for ewes that had previously produced a lamb than for ewes that had been barren the previous year (table 2) because some individuals failed to lactate in consecutive years. Fertility decreased with increasing population density (table 2). The final model, which includes the effects of density and previous reproductive success, accounted for 22.8% of variation in fertility.

When we restricted the analysis to individual ewes with at least 5 yr of data ($N = 273$ ewe-years), the logistic regression model selected for the overall data set (suggesting that the effect of ewe mass on fertility increased with both density and fertility the previous year) remained significant ($\chi^2 = 27.39$, df $= 9$, $P = .001$) and the effect of female identity was not significant ($\chi^2 = 34.67$, df $= 39$, $P = .67$).

Lamb Survival to Weaning. Lamb survival to weaning ($N = 500$ lambs) increased with maternal mass for ewes that had produced lambs the previous year (table 3). At all levels of density, weaning success was lower for ewes that had weaned lambs the previous year than for ewes that had not weaned lambs, indicating a reproductive cost of lactation. Reproductive costs increased with population density, and this increase was greater for light ewes than for heavy ewes (table 3). Heavy ewes that had weaned a lamb the previous year had roughly similar weaning success at any density, but as density increased,

Table 1: Model selection for survival of bighorn sheep ewes aged 4–14 yr on Ram Mountain, 1973–1997

Model	Deviance	df	Difference in deviance between models compared		Difference in df between models compared	P value of likelihood ratio test
(1) Null model: Logit (S) = constant	345.9	582	. . .		. . .	. . .
(2) General model: Logit (S) = $A \times D \times R \times M$	286.5	548	(1) and (2):	59.5	34	.004
(3): (2) − $A \cdot D \cdot R \cdot M$	292.1	551	(2) and (3):	5.7	3	.13
(4): (3) − $A \cdot R \cdot M$	298.2	553	(3) and (4):	6.1	2	.047
(5): (3) − $A \cdot D \cdot M$	298.2	553	(3) and (5):	6.1	2	.047
(6): (3) − $R \cdot D \cdot M$	298.1	555	(3) and (6):	6.0	4	.20
(7): (3) − $A \cdot R \cdot D$	300.8	555	(3) and (7):	8.7	4	.069
A. Prime-aged ewes (4–7 yr):						
(1′) Null model	148.8	359	. . .		. . .	. . .
(2′) General model	136.6	342	(1′) and (2′):	12.2	17	.79
(3′): (2′) − $R \cdot D \cdot M$	142.4	346	(2′) and (3′):	5.8	4	.22
(4′): (3′) − $R \cdot M$	142.4	348	(3′) and (4′):	.03	2	.99
(5′): (3′) − $R \cdot D$	142.8	350	(3′) and (5′):	.4	4	.98
(6′): (3′) − $M \cdot D$	143.7	348	(3′) and (6′):	1.3	2	.52
(7′) Logit (S') = $D + R + M$	144.0	354	. . .		. . .	. . .
(8′): (7′) − D	144.2	356	(7′) and (8′):	.2	2	.94
(9′): (7′) − R	148.1	358	(7′) and (9′):	4.1	2	.13
(10′): (7′) − M	144.0	355	(7′) and (10′):	.0	1	>.99
Model selected: Logit (S') = constant	. . .	. . .	. . .		. . .	. . .
B. Senescent ewes (8–14 yr):						
(1″) Null model	183.4	222	. . .		. . .	. . .
(2″) General model	149.8	206	(1″) and (2″):	33.6	16	.006
(3″): (2″) − $R \cdot D \cdot M$	155.7	209	(2″) and (3″):	5.9	3	.12
(4″): (3″) − $R \cdot M$	160.2	211	(3″) and (4″):	4.5	2	.11
(5″): (3″) − $R \cdot D$	165.7	213	(3″) and (5″):	10.0	4	.039
(6″): (3″) − $M \cdot D$	161.4	211	(3″) and (6″):	5.7	2	.056
Model selected: Logit (S'') = $R + D + M +$ $R \cdot D + M \cdot D$	. . .	. . .	. . .		. . .	. . .

Note: For each model (numbered within parentheses), the table gives the terms included in the model, the deviance, the number of degrees of freedom, the difference in deviance and in df between models to be compared, and the P values of the likelihood-ratio tests (see text for details about the testing procedure). The models compared at each step and the model selected at the end of the analysis are indicated. A = ewe age; D = population density; R = reproductive success the previous year; M = ewe mass; S = survival; $X \times Y$ = cumulative effects of factors X and Y as well as their interaction; $X \cdot Y$ = interaction between X and Y.

light ewes that had just weaned a lamb found it increasingly difficult to wean another lamb. Ewe age did not affect lamb survival to weaning (table 3). The final logistic model explained only 7.5% of the variability in lamb survival to weaning, which averaged 69.4%.

When we restricted the analysis to ewes with at least 5 yr of data (N = 222 ewe-years), the logistic regression model selected for the overall data set (suggesting that the positive effect of ewe mass on lamb survival to weaning increased with both density and previous reproductive success) remained significant (χ^2 = 25.63, df = 9, P = .002), and there was a significant effect of female identity (χ^2 = 49.38, df = 30, P = .014). This result indicates that, once the effects of mass, previous reproductive success, and population density were accounted for,

individual females tended consistently either to succeed or to fail at weaning lambs over their lifetime.

Lamb Survival to 1 Yr. Winter survival of weaned lambs (N = 293) was independent of either ewe mass, age, or previous reproductive success but revealed a strong negative effect of density (table 4), confirming our earlier analyses (Festa-Bianchet et al. 1997). Over the entire study, 60.8% of marked lambs whose mother was identified survived the winter, but lamb survival dropped precipitously over the three levels of density (fig. 1). The final model explained 11.2% of variation in lamb survival from weaning to 1 yr.

When we restricted the analysis to ewes with at least 5 yr of data (N = 77 ewe-years), the logistic regression

Table 2: Model selection for fertility of bighorn sheep ewes on Ram Mountain

Model	Deviance	df	Difference in deviance between models compared	Difference in df between models compared	P value of likelihood ratio test
(1) Null model: Logit (P) = constant	349.3	552	. . .	. . .	. . .
(2) General model: Logit $(P) = M \times R \times D$	256.4	535	(1) and (2): 92.9	17	<.001
(3): (2) $- M \cdot R \cdot D$	264.7	539	(2) and (3): 8.3	4	.082
(4): (3) $- R \cdot D$	269.7	543	(3) and (4): 5.0	4	.28
(5): (3) $- R \cdot M$	270.6	541	(3) and (5): 5.9	2	.051
(6): (3) $- D \cdot M$	273.8	541	(3) and (6): 9.1	2	.011
(7) Model selected: Logit $(P) = M \times D + M \times R$	269.7	543	. . .	. . .	. . .
(8): (7) $+ A$	260.7	553	(7) and (8): 9.0	10	.53
(9): (7) $+ A \cdot M$	253.8	524	(7) and (9): 6.9	9	.65

Note: See table 1 for notations. P = probability of reproductive success.

model selected for the overall data set (with a negative effect of density on lamb survival) remained significant (χ^2 = 9.70, df = 1, P = .002) but the effect of female identity was not significant (χ^2 = 9.90, df = 12, P = .62). Therefore, postweaning survival was strongly affected by density but appeared independent of maternal characteristics such as mass, age, and previous reproduction.

Effects of Reproductive Success, Age, and Density on Changes in Ewe Mass

At ages 4–7 yr, body mass generally increased if the ewe did not lactate or if her lamb died before weaning, while for older ewes the effects of reproductive success on changes in body mass were weaker (fig. 2), suggesting that the somatic costs of reproduction were greater for prime-aged than for older ewes. There was an almost sig-

nificant interaction of reproductive success and density: as density increased, barren females tended to show a greater positive change in mass from the previous year, while females that weaned lambs tended to show a greater negative change in mass (table 5, fig. 2).

An analysis including only ewes with at least 5 yr of data (N = 301 ewe-years) did not reveal any effect of female identity when age, reproductive success, and density, as well as the significant interactions among these factors, were accounted for (F = 0.33, df = 41, 225, $P >$ .99). Therefore, there were no consistent individual differences in the somatic costs of reproduction.

Discussion

Measurable reproductive costs and trade-offs between different components of reproductive success in bighorn ewes vary with population density and individual mass.

Table 3: Model selection for lamb survival to weaning

Model	Deviance	df	Difference in deviance between models compared	Difference in df between models compared	P value of likelihood ratio test
(1) Null model: Logit (P) = constant	615.9	499	. . .	. . .	. . .
(2) General model: Logit $(P) = M \times R \times D$	558.5	483	(1) and (2): 57.4	16	<.001
(3): (2) $- M \cdot R \cdot D$	563.4	486	(2) and (3): 4.9	3	.18
(4): (3) $- R \cdot D$	569.6	490	(3) and (4): 6.2	4	.18
(5): (3) $- R \cdot M$	572.7	488	(3) and (5): 9.3	2	.009
(6): (3) $- D \cdot M$	569.0	488	(3) and (6): 5.6	2	.059
(7) Selected model: Logit $(P) = M \times D + M \times R$	569.6	490	. . .	. . .	. . .
(8): (7) $+ A$	558.2	480	(7) and (8): 11.4	10	.33
(9): (7) $+ A \cdot M$	548.2	471	(7) and (9): 10.0	9	.35

Note: See table 1 for notations. P = probability of reproductive success.

Table 4: Model selection for lamb survival to 1 yr

Model	Deviance	df	Difference in deviance between models compared	Difference in df between models compared	P value of likelihood ratio test
(1) Null model: Logit $(P) =$ constant	392.5	292	. . .	. . .	. . .
(2) General model: Logit $(P) = M \times R \times D$	333.1	275	(1) and (2): 59.4	17	<.001
(3): (2) $- M \cdot R \cdot D$	335.6	279	(2) and (3): 2.5	4	.65
(4): (3) $- R \cdot D$	339.6	283	(3) and (4): 4.0	4	.40
(5): (3) $- R \cdot M$	337.8	281	(3) and (5): 2.2	2	.32
(6): (3) $- D \cdot M$	339.0	281	(3) and (6): 3.4	2	.18
(7): Logit $(P) = M + D + R$	345.9	287	. . .	. . .	. . .
(8): (7) $- M$	346.3	288	(7) and (8): .4	1	.55
(9): (7) $- R$	347.8	289	(7) and (9): 1.9	2	.40
(10): (7) $- D$	386.4	289	(7) and (10): 40.5	2	<.001
(11) Selected model: Logit $(P) = D$	348.4	290	. . .	. . .	. . .
(8): (7) $+ A$	340.1	280	(7) and (8): 8.3	10	.60
(9): (7) $+ A \cdot M$	327.2	268	(7) and (9): 12.9	12	.37

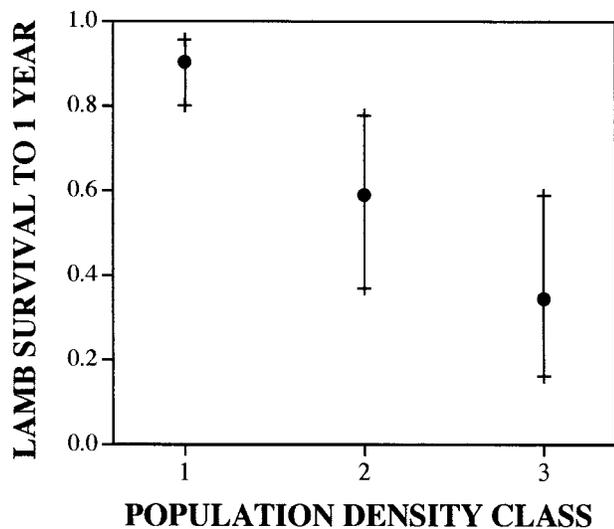Note: See table 1 for notations. $P =$ probability of reproductive success.

Figure 1: Bighorn lamb survival from weaning to 1 yr (mean and 95% confidence intervals for a binomial distribution) according to population density. Density level 1 indicates lambs born at low density whose mothers were born at low density, level 2 indicates lambs born at high density whose mothers were born at low density, and level 3 indicates lambs born at high density whose mothers were born at high density. The data refer only to lambs whose mothers were included in the analysis reported in the text. Sample sizes were 62, 173, and 58 lambs for increasing levels of density.

As expected, mass had a positive effect on reproductive success, but that effect varied with density. At low density, reproductive success was mostly independent of body mass and reproductive costs were low. As density increased, reproduction became increasingly difficult for light ewes, but the reproductive success of the heaviest ewes was largely unaffected by either density or previous reproductive expenditure.

Individual mass can be affected by skeletal size and fat accumulation. Differences in fat stores would affect body condition and should play an important role in reproductive success (Clutton-Brock et al. 1997). Because mass differences among ewes (individuals ranged in mass from 55 to 85 kg) were much greater than yearly mass changes within individuals (fig. 2), interindividual mass differences can be largely attributed to differences in skeletal size: heavy ewes were generally larger than light ewes, not just fatter. Larger ewes could have a reproductive advantage at high population density because of lower relative food requirements and thermoregulatory costs relative to lighter ewes. Lower relative metabolic rates may also allow large ewes to be more efficient than small ewes at converting food into fat reserves. In addition, litter size is fixed at one and maternal mass has little effect on lamb mass at weaning, suggesting that relative reproductive expenditure decreases with increasing ewe mass (Festa-Bianchet and Jorgenson 1998).

Large ewes could be socially dominant. Positive association between female dominance and reproductive success has been reported for other ungulates (Clutton-Brock et al. 1986; Green et al. 1989) but not for bighorn ewes, despite several studies that have examined domi-
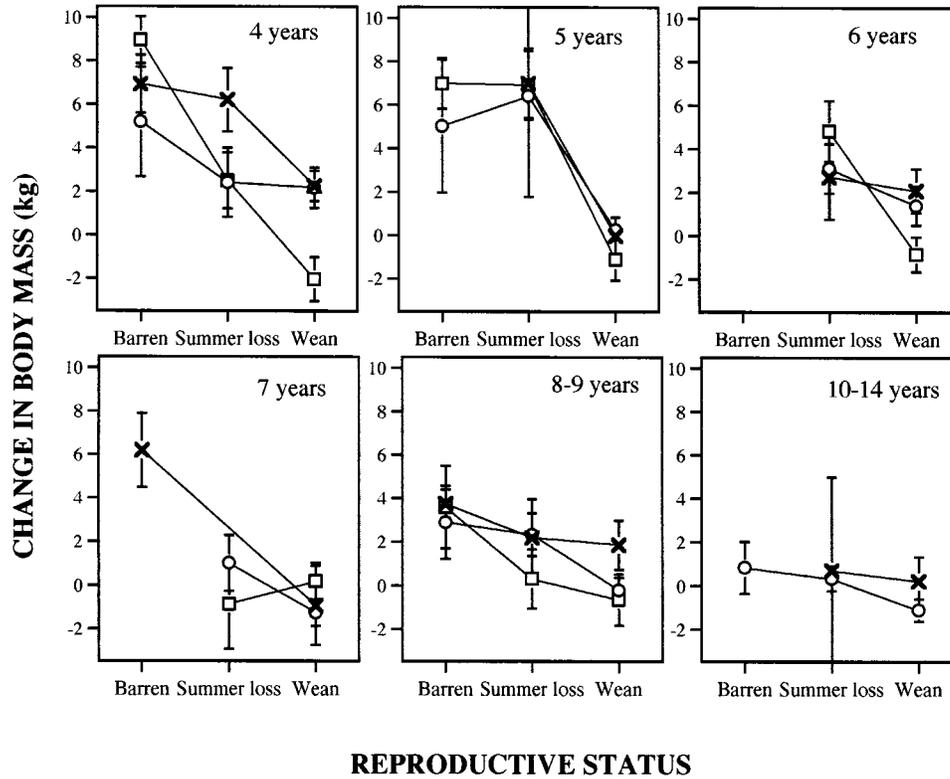
REPRODUCTIVE STATUS

Figure 2: Effects of age, population density, and reproduction on mass change from 1 yr earlier for bighorn ewes on September 15. The average ±SD of change in kilograms is shown. Ewes born and reproducing at low density are represented by crosses, ewes born at low density and reproducing at high density are represented by circles, and ewes born and reproducing at high density are represented by open squares. Only cases with sample size of at least two are reported; sample sizes ranged from two to 67 and averaged 14 ± 12.7 SD.

nance and reproduction in this species (Eccles and Shackleton 1986; Festa-Bianchet 1991; Hass 1991). Social behavior appears unlikely to affect mass-related differences in reproductive success of bighorn ewes, although no study of this species has examined the potential effects of dominance under resource scarcity. The costs of reproduction were most evident at high population den-

sity: the benefits of dominance may also only be evident at high density.

There is clear evidence that at Ram Mountain resources were limited at high density: as population density increased, lactating ewes gained less mass (fig. 2), the age of primiparity increased (Jorgenson et al. 1993*a*), and survival decreased for yearling ewes (Jorgenson et al.

Table 5: Model selection for change in mass adjusted to September 15 from 1 yr earlier for bighorn ewes aged 4–14 yr at Ram Mountain, 1973–1997

Tests of hypothesis	F-*test*	df	P *value*
General model: $C = \overline{X} + A \times D \times R$	· · ·	· · ·	· · ·
Test of the three-way interaction $A \cdot D \cdot R$	1.35	21,542	.135
Test of the two-way interaction $A \cdot D$	1.04	15,563	.410
Test of the two-way interaction $A \cdot R$	1.69	19,563	.033
Test of the two-way interaction $D \cdot R$	2.31	4,563	.057
Selected model: $C = \overline{X} + A \times R + R \times D$	· · ·	· · ·	· · ·

Note: A three-way ANOVA was performed. In the general model, the change in mass (C) is equal to a mean ($\overline{X}$) affected by a three-way interaction of ewe age (A), population density (D), and reproductive success (R).

1997) and for lambs (Festa-Bianchet et al. 1997). When density was artificially kept low, mid-September mass had no measurable effect on reproductive success the following year. At high density, however, there was a reproductive advantage to being heavy. Although somatic and fitness costs of lactation were evident at all levels of population density, these costs increased with density. In this population, early primiparity only became costly at high density (Festa-Bianchet et al. 1995). Our long-term research illustrates how temporal variation in resource availability affects reproductive costs and must be included when considering what selective pressures may affect the evolution of life-history strategies. In long-lived mammals, individuals may encounter widely different levels of resource availability during their lifetime: this situation should select for a flexible and conservative strategy of maternal expenditure, as any one single reproductive strategy is unlikely to be optimal throughout the life of an individual (Clutton-Brock et al. 1996; Festa-Bianchet and Jorgenson 1998).

Analyses of ewe mass, survival, longevity, and reproductive success (Jorgenson et al. 1993a; Festa-Bianchet et al. 1995, 1997; Bérubé et al. 1996; Bérubé 1997) have so far failed to reveal any costs of large mass: all of our results suggest that heavy ewes are advantaged over light ones. Although negative results do not exclude the existence of trade-offs between mass and some fitness component, it seems likely that many ewes are light because they cannot accumulate more mass rather than because heterogeneity in mass is maintained by selection. If large ewes incurred a cost because their absolute food requirements are greater than for small ewes, there should be a negative effect of large size when food is scarce. Instead, the reproductive advantage of large size was most evident at high density.

The different effects of reproduction on changes in body mass according to population density (fig. 2) are further evidence that the costs of reproduction vary according to resource availability. At high density, ewes born at high density gained more mass than ewes born at low density if they were barren, but the reverse was true for ewes that weaned lambs. Therefore, ewes born at high density appeared to experience greater somatic costs of reproduction than ewes born at low density. Population density during a given reproductive episode and during early development appeared to have a cumulative effect on the costs of reproduction. We now plan to reduce population density to monitor the reproductive performance of ewes born at high density and reproducing at low density.

The increasing cost of reproduction with population density may explain why, as density increased, light ewes became less likely to reproduce, as reported for other ungulates and from an analysis of age of primiparity for Ram Mountain bighorns (Albon et al. 1983; Jorgenson et al. 1993a). The decrease in lamb survival to weaning for light ewes at high population density, however, is unlikely to be an adaptive response to low resource availability. We have no evidence that ewes abandoned their lambs, but as proximate causes of lamb death were seldom known, we cannot exclude that possibility. In a cyclic feral population of domestic sheep, Clutton-Brock et al. (1996) found little evidence that ewes adjusted annual reproductive effort to resource availability, despite wide density-dependent changes in reproductive costs. High fertility despite fluctuating resource availability may be a common characteristic of different species of sheep: these animals do not appear to adopt a tracking strategy of reproductive investment.

Our data suggest that bighorn ewes are "capital breeders" (Stearns 1992; Jönsson 1997) because mass affected reproduction and reproduction affected mass. Food availability during lactation, however, is also likely to play an important role in reproductive success by affecting summer mass gain, which in turn affects reproduction the following year. By taking into account individual differences in mass and by considering the effects of density, we demonstrated a cost of reproduction: lactation had a negative effect on ewe mass, and reproductive success the following year was negatively affected by small mass in late summer.

Lamb production was the only component of reproduction for which we found a positive association in consecutive years. Apparently, some ewes are unlikely to lactate (and, presumably, to conceive) for reasons independent of the variables we examined. Interesting, failure to reproduce for older ewes was associated with low survival, and this effect increased with density. It appears that the factors that caused some ewes not to produce lambs also decreased their viability after 8 yr of age. Experimental manipulations of reproductive effort are needed to reveal what these factors may be.

Our analysis of the interactions of ewe age, density, and reproductive effort on ewe survival revealed a negative effect of population density on the survival of senescent ewes that failed to wean lambs. This is an important result because it underlines the need to distinguish among different age classes for demographic studies of long-lived mammals, rather than lumping all nonjuveniles into a single "adult" age class. Our previous analyses of survival in several populations of ungulates stressed the importance of this distinction but did not take reproductive status into account and failed to reveal density dependence in the survival of prime-aged or senescent females (Jorgenson et al. 1997; Gaillard et al. 1998). However, our results do not suggest that density-dependent mortality in older ewes is a cost of reproduction, probably because heterogeneity in individual quality, including

body mass, affects life expectancy of bighorn females (Bérubé 1997). On the contrary, the positive covariation of reproductive success and survival for ewes older than 8 yr is likely to increase variance in female lifetime reproductive success.

In the Sheep River population of bighorn sheep, a nonsignificant positive association between reproductive success of the same ewe in consecutive years was found (Festa-Bianchet 1989). The Sheep River population did not vary in density as much as the Ram Mountain population and has shown little evidence of resource limitation. At Ram Mountain, we found negative effects of gestation and particularly of lactation on weaning success the following year.

These apparently conflicting results for two populations of the same species may be due to differences in body mass, and further support the argument that reproductive costs in large mammals are expressed only for individuals that cannot obtain sufficient resources. Ewes at Sheep River winter at low elevation and have access to nutritious growing forage several weeks earlier than ewes at Ram Mountain. Bighorns at Sheep River are among the heaviest in North America (Blood et al. 1970). Three adult ewes captured at Sheep River in autumn weighed 74, 78, and 80 kg, compared to an average of about 70 kg for Ram Mountain ewes. Reproduction should be less costly at Sheep River than at Ram Mountain because most ewes at Sheep River are as heavy as the heaviest Ram Mountain ewes, for which we found little evidence of fitness costs of reproduction. Negative effects of reproduction in a particular year on reproduction the following year were also reported for red deer (*Cervus elaphus*) in a high-density population in marginal habitat (Clutton-Brock et al. 1983). Studies of different populations of American bison have reported widely different costs of lactation (Berger 1989; Green 1990), and no costs of reproduction were found in pronghorn (*Antilocapra americana*) in a population apparently not limited by food (Byers 1997). In Columbian ground squirrels (*Spermophilus columbianus*), litter size was correlated with fitness costs during a population decline but not while the same population was increasing (Festa-Bianchet and King 1991). Studies of Columbian ground squirrels in areas where resources were apparently not limited failed to reveal strong fitness costs of reproduction (Murie and Dobson 1987; Hare and Murie 1992). It is therefore likely that for many mammals the costs of reproduction in females are evident only for individuals that are in poor condition, either because they are small or because they are in high-density populations.

The results reported here, those in an earlier study (Festa-Bianchet 1989), and those in several nonmanipulative studies reported above are not an accurate measure of the fitness costs of reproduction because they do not fully account for individual differences in reproductive potential (Reznick 1985, 1992). Our results, however, suggest that reproduction (particularly lactation) is costly and that the costs of reproduction are affected by an interaction of body mass and population density. By taking individual mass into account, we partially accounted for individual differences in reproductive potential (van Noordwijk and de Jong 1986). In particular, we detected a cost of reproduction even in the presence of some mass-independent individual differences in reproductive ability, which were revealed by the individual-level analysis of weaning success. Comparisons of reproductive success with individual mass and resource availability are a promising avenue of research into reproductive strategies of capital breeders. Our work underlines the usefulness of long-term field studies of long-lived mammals for our understanding of the evolution of life histories. Continued monitoring of marked individuals and experimental manipulations of reproductive effort are now required to further investigate how mass, density, age, and individual reproductive potential affect reproductive strategies.

Literature Cited

Albon, S. D., B. Mitchell, and B. W. Staines. 1983. Fertility and body weight in female red deer: a density-dependent relationship. Journal of Animal Ecology 52: 969–980.

Berger, J. 1989. Female reproductive potential and its ap-

parent evaluation by male mammals. Journal of Mammalogy 70:347–358.

Bérubé, C. H. 1997. Les stratégies d'adaptation vitale chez les brebis du mouflon d'Amérique (*Ovis canadensis*): la reproduction en fonction de l'âge. Ph.D. diss. Université de Sherbrooke, Sherbrooke.

Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behavioral Ecology 7: 60–68.

Blood, D. A., D. R. Flook, and W. D. Wishart. 1970. Weights and growth of Rocky Mountain bighorn sheep in western Alberta. Journal of Wildlife Management 34:451–455.

Byers, J. A. 1997. American pronghorn. University of Chicago Press, Chicago.

Calder, W. A. 1984. Size, function and life history. Cambridge University Press, Cambridge.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

Campbell, M. T., and N. A. Slade. 1995. The effect of maternal mass on litter size and offspring survival in the hispid cotton rat (*Sigmodon hispidus*). Canadian Journal of Zoology 73:133–140.

Carranza, J. 1996. Sexual selection for male body mass and the evolution of litter size in mammals. American Naturalist 148:81–100.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology 52:367–383.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1986. Great expectations: dominance, breeding success and offspring sex ratio in red deer. Animal Behaviour 34:460–471.

Clutton-Brock, T. H., I. R. Stevenson, P. Marrow, A. D. MacColl, A. I. Houston, and J. M. McNamara. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. Journal of Animal Ecology 65:675–689.

Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. American Naturalist 149:195–219.

Eccles, T. R., and D. M. Shackleton. 1986. Correlates and consequences of social status in female bighorn sheep. Animal Behaviour 34:1392–1401.

Festa-Bianchet, M. 1988. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. Animal Behaviour 36:1445–1454.

———. 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). Journal of Animal Ecology 58:785–795.

———. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Animal Behaviour 42:71–82.

Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144–150.

Festa-Bianchet, M., and W. J. King. 1991. Effects of litter size and population dynamics on juvenile and maternal survival in Columbian ground squirrels. Journal of Animal Ecology 60:1077–1090.

Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871–881.

Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. Canadian Journal of Zoology 74:330–342.

Festa-Bianchet, M., J. T. Jorgenson, C. H. Bérubé, C. Portier, and W. D. Wishart. 1997. Body mass and survival of bighorn sheep. Canadian Journal of Zoology 75:1372–1379.

Francis, B., M. Green, and C. Payne. 1993. The GLIM system, release 4 manual. Clarendon, Oxford.

Gaillard, J.-M., A. J. Sempéré, J.-M. Boutin, G. V. Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Canadian Journal of Zoology 70:1541–1545.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Green, W. C. H. 1990. Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? Behavioral Ecology 1:148–160.

Green, W. C. H., and A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. Oecologia (Berlin) 86:521–527.

Green, W. C. H., J. G. Griswold, and A. Rothstein. 1989. Post-weaning associations among bison mothers and daughters. Animal Behaviour 38:847–858.

Hansson, L. 1992. Fitness and life history correlates of weight variations in small mammals. Oikos 64:479–484.

Hare, J. F., and J. O. Murie. 1992. Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. Journal of Mammalogy 73:449–454.

Hass, C. C. 1991. Social status in female bighorn sheep (*Ovis canadensis*): expression, development and reproductive correlates. Journal of Zoology (London) 225: 509–523.

Hewison, A. J. M. 1996. Variation in the fecundity of roe

deer in Britain: effects of age and body weight. Acta Theriologica 41:187–198.

Hogg, J. T., C. C. Hass, and D. A. Jenni. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. Behavioral Ecology and Sociobiology 31: 243–251.

Humphries, M. M., and S. Boutin. 1996. Reproductive demands and mass gains: a paradox in female red squirrels (*Tamiasciurus hudsonicus*). Journal of Animal Ecology 65:332–338.

Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993a. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. Canadian Journal of Zoology 71:2509–2517.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993b. Harvesting bighorn ewes: consequences for population size and trophy ram production. Journal of Wildlife Management 57:429–435.

Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78: 1019–1032.

King, W. J., M. Festa-Bianchet, and S. E. Hatfield. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia (Berlin) 86:528–534.

Kojola, I., and T. Helle. 1993. Calf harvest and reproductive rate of reindeer in Finland. Journal of Wildlife Management 57:451–453.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Machlis, L., P. W. D. Dodd, and J. C. Fentress. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie 68:201–214.

Marrow, P., J. M. McNamara, A. I. Houston, I. R. Stevenson, and T. H. Clutton-Brock. 1996. State-dependent life history evolution in Soay sheep: dynamic modeling of reproductive scheduling. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351:17–32.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature (London) 380:215–221.

Michener, G. R. 1989. Reproductive effort during gestation and lactation by Richardson's ground squirrels. Oecologia (Berlin) 78:77–86.

Millar, J. S., E. M. Derrickson, and S. T. P. Sharpe. 1992. Effects of reproduction on maternal survival and subsequent reproduction in northern *Peromyscus maniculatus*. Canadian Journal of Zoology 70:1129–1134.

Morris, D. W. 1996a. State-dependent life histories, Mountford's hypothesis, and the evolution of brood size. Journal of Animal Ecology 65:43–51.

———. 1996b. State-dependent life history and senescence of white-footed mice. Écoscience 3:1–6.

Murie, J. O., and F. S. Dobson. 1987. The costs of reproduction in female Columbian ground squirrels. Oecologia (Berlin) 73:1–6.

Partridge, L. 1992. Measuring reproductive costs. Trends in Ecology & Evolution 7:99–100.

Partridge, L., and P. H. Harvey. 1988. The ecological context of life history evolution. Science (Washington, D.C.) 241:1449–1455.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Reimers, E. 1983. Reproduction in wild reindeer in Norway. Canadian Journal of Zoology 61:211–217.

Reiter, J., and B. J. LeBoeuf. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28:153–160.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

———. 1992. Measuring the costs of reproduction. Trends in Ecology & Evolution 7:42–45.

Sæther, B.-E., and H. Haagenrud. 1983. Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. Journal of Mammalogy 64: 226–232.

Schemper, M. 1990. The explained variation in proportional hazards regression. Biometrika 77:216–218.

Searle, S. R. 1971. Linear models. Wiley, New York.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Sydeman, W. J., H. R. Huber, S. D. Emslie, C. A. Ribic, and N. Nur. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology 72:2204–2217.

van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128: 137–142.

Wauters, L. A., and A. A. Dhondt. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos 72:402–410.

Associate Editor: John A. Byers