

Individual variation in reproductive costs of reproduction: high-quality females always do better

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Summary

1. Although life-history theory predicts substantial costs of reproduction, individuals often show positive correlations among life-history traits, rather than trade-offs. The apparent absence of reproductive costs may result from heterogeneity in individual quality.

2. Using detailed longitudinal data from three contrasted ungulate populations (mountain goats, *Oreamnos americanus*; bighorn sheep, *Ovis canadensis*; and roe deer, *Capreolus capreolus*), we assessed how individual quality affects the probability of detecting a cost of current reproduction on future reproduction for females. We used a composite measure of individual quality based on variations in longevity (all species), success in the last breeding opportunity before death (goats and sheep), adult mass (all species), and social rank (goats only).

3. In all species, high-quality females consistently had a higher probability of reproduction, irrespective of previous reproductive status. In mountain goats, we detected a cost of reproduction only after accounting for differences in individual quality. Only low-quality female goats were less likely to reproduce following years of breeding than of nonbreeding. Offspring survival was lower in bighorn ewes following years of successful breeding than after years when no lamb was produced, but only for low-quality females, suggesting that a cost of reproduction only occurred for low-quality females.

4. Because costs of reproduction differ among females, studies of life-history evolution must account for heterogeneity in individual quality.

Key-words: annual reproductive success, bighorn sheep, mountain goat, roe deer, weaning

Introduction

The principle of energy allocation (Williams 1966) is central to life-history theory. Because energy and time are limited, individuals should allocate resources optimally among maintenance, growth, and reproduction to maximize fitness (Stearns 1992). If reproductive effort reduces the availability of resources for somatic allocation, females should face a trade-off between current reproduction and subsequent reproductive potential (Stearns 1992), leading to a cost of reproduction. The most commonly reported cost is a reduced probability of reproduction the following year. For instance, female moose (*Alces alces* Linnaeus) that weaned a calf had reduced fecundity the following year compared with females that did not wean a calf (Testa 2004). Similar results have been found in other studies (e.g. Clutton-Brock, Guinness & Albon 1983; Boyd *et al.* 1995; Huber *et al.* 1999). Reproductive costs

are often due to reduced body condition resulting from investment in current reproduction (Testa & Adams 1998; Pomeroy *et al.* 1999; Bonnet *et al.* 2002).

Several studies, however, reported positive associations between current and future reproduction (Clutton-Brock *et al.* 1996; Bonnet *et al.* 2002; Weladji *et al.* 2008). In kittiwakes (*Rissa tridactyla* Linnaeus; Cam *et al.* 1998) and fur seals (*Arctocephalus tropicalis* Gray; Beauplet *et al.* 2006), for example, breeders had higher survival and breeding probabilities in subsequent years than nonbreeders. The apparent absence of costs of reproduction may be due to the ability of individuals to increase nutrient intake and compensate for these costs (Tuomi, Hakala & Haukioja 1983; Bonnet *et al.* 2002). Alternatively, if individuals are adapted to moderate resource deficiencies, the costs of reproduction may only be evident when resources are limited or population density is high (Tuomi *et al.* 1983; Clutton-Brock *et al.* 1996; Toïgo *et al.* 2002; Török *et al.* 2004). Costs of reproduction could also be masked by phenotypic variations among individuals,

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Table 1. Summary of indices characterizing heterogeneity among individuals (HI), which were used in the analyses for each species of large herbivore. The gradient of negative to positive values on each index represents a gradient of low- to high-quality females

	Description of the individual quality index
Mountain goats – HI-1 (scores of PCA axis 1)	Gradient of females that were light and subordinate (negative values) to females that were heavy and dominant (positive values)
Mountain goats – HI-2 (scores of PCA axis 2)	Gradient of females that were short-lived, failed in their last breeding opportunity, and tended to be light and subordinate (negative values) to females that were long-lived, succeeded in their last breeding attempt, and tended to be heavy and dominant (positive values)
Bighorn sheep – HI (scores of PCA axis 1)	Gradient of females that were short-lived, failed in their last breeding opportunity, and tended to be light (negative values) to females that were long-lived, succeeded in their last breeding attempt, and tended to be heavy (positive values)
Roe deer – HI (scores of an orthogonal regression between longevity and body mass*)	Gradient of females that were short-lived and light (negative values) to females that were long-lived and heavy (positive values)

*Because there was only two life-history traits available for roe deer, that is, longevity and body mass, we performed an orthogonal regression between these two variables and used the scores of the regression as an index of female quality. This approach is similar to conducting a PCA with two variables and using the scores of the first axis.

such as differences in body condition (Reznick 1985; Doughty & Shine 1997; Bérubé, Festa-Bianchet & Jorgenson 1999), previous experience, social rank, or age (McNamara & Houston 1996), resulting in differential costs of reproduction among individuals. There may be a threshold under which somatic costs do not cause any fitness costs of reproduction, and this threshold could vary with individual quality or physiological state (Tuomi *et al.* 1983; Doughty & Shine 1997). Manipulative experiments that control for individual variations in resource availability and energy allocation can quantify reproductive costs (Partridge & Harvey 1985; Reznick 1985). For large mammals, however, manipulations are nearly impossible (see Tavecchia *et al.* 2005 for an exception in Soay sheep, *Ovis aries* Linnaeus), and thus a surrogate of individual quality should be used to account for heterogeneity among individuals.

Here we assessed the influence of individual quality on the probability of detecting a cost of reproduction in terms of future reproduction in three intensively monitored populations of ungulates: mountain goats (*Oreamnos americanus* De Blainville), bighorn sheep (*Ovis canadensis* Shaw), and roe deer (*Capreolus capreolus* Linnaeus). We used a composite measure of individual quality based on variations in life-history traits that could influence fitness, including longevity, success in the last breeding opportunity before death, adult mass, and social rank (some variables were not available for all species; see Methods and Table 1). Because high-quality individuals should have a greater probability of reproducing in successive breeding opportunities than low-quality individuals, reproductive costs should become evident after accounting for heterogeneity in individual quality.

Materials and methods

STUDY AREAS AND POPULATIONS

We studied mountain goats at Caw Ridge (54°03' N, 119°23' W), bighorn sheep at Ram Mountain (52°20' N, 115°45' W), both in Alberta, Canada, and roe deer at Trois-Fontaines (48°42' N, 4°55' E), France. Caw Ridge is in the foothills of the Rocky Mountains,

whereas Ram Mountain is isolated from these mountains by ~30 km. Goats and sheep use respectively 28 km² and 38 km² of alpine tundra and subalpine open forest of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* Hook) at about 1750–2200 m elevation. The climate is characterized by long, cold winters and short, cool summers. Snowfall can occur during any month. Trois-Fontaines is an enclosed forest (~14 km²) composed of oak (*Quercus* spp. L.), beech (*Fagus sylvatica* L.), hornbeam (*Carpinus betulus* L.), ivy (*Hedera helix* L.), and bramble (*Rubus* sp. L.). The climate is continental, with cool winters and hot summers.

We used longitudinal data collected on individually marked females between 1988 and 2006 for goats, and between 1975 and 2006 for sheep and deer. Most females were marked (over 98% in goats and sheep, and about 70% in deer) with visual collars and colour-coded ear tags. We captured mountain goats and bighorn sheep in May–October in box and corral traps, respectively. Roe deer were captured in January–February using drive nets. We weighed individuals at capture. We collected additional body masses of goats and sheep without handling animals using electronic platform scales baited with salt. All females were of known age because they were first captured as juveniles. Because we required lifetime data to determine female quality (see below), we only included in the analyses cohorts with complete lifetime data (i.e. all individuals had died) and females that died of natural causes (goats: $n = 23$ females; sheep: $n = 123$; deer: $n = 84$).

During the study, the mountain goat population increased from about 80 to 160 individuals. The bighorn sheep population first increased from about 100 to 230 individuals, then declined steeply in the 1990s, and remained at about 40–50 sheep since 2000. The roe deer population varied between about 160 and 400 individuals. In all analyses, population density refers to the total number of individuals in 1 year (only animals > 1 year of age for roe deer because estimates of fawn numbers were not available for all years). Details on study areas and populations are published elsewhere (Gaillard *et al.* 1998; Festa-Bianchet, Jorgenson & Réale 2000; Côté & Festa-Bianchet 2001a, b).

REPRODUCTION

Mountain goats and bighorn sheep are capital breeders, relying heavily on body reserves for the high energetic needs of reproduction (Festa-Bianchet, Gaillard & Jorgenson 1998; Côté & Festa-Bianchet 2001a). At Caw Ridge and Ram Mountain, female goats and sheep gave birth to a single offspring in late May/early June, and weaned offspring in September. Most female goats were primiparous at 4 or

5 years of age (Côté & Festa-Bianchet 2001b), whereas female sheep were usually primiparous at 2 or 3 years old but delayed reproduction until 4 or 5 years old at high density (Jorgenson *et al.* 1993; Festa-Bianchet *et al.* 1995). Mountain goats skipped annual reproduction much more commonly ($\approx 25\%$ of years) than bighorn sheep ($\approx 10\%$). In contrast, roe deer are income breeders, relying almost exclusively on available food resources for reproduction (Andersen *et al.* 2000). At Trois-Fontaines, female deer usually gave birth to twins, and occasionally to triplets, in April–May and weaned them in late August. All females were primiparous at 2 years of age and almost never skipped reproduction (Gaillard *et al.* 1998).

For goats and sheep, we determined the annual reproductive status of each female from observations of nursing behaviour during intensive censuses from mid-May to late September. Because detection probability was 100% for both species (Festa-Bianchet, Gaillard & Côté 2003), females not seen 1 year were assumed to be dead. We divided annual reproductive status in three categories: (1) 'no offspring', if a female did not reproduce; (2) 'offspring died before weaning', if the offspring died before late September; and (3) 'offspring survived to weaning', if the offspring survived until late September. Analyses comparing females that reproduced (categories 2 and 3 combined) with females that did not reproduce provided a much better fit in goats ($\Delta\text{QICu} \geq 3$; see Statistical Analyses) and were equivalent in sheep ($\Delta\text{QICu} \leq 2$) to models with three categories. Therefore, we only present results using two reproductive states, that is, offspring produced vs. no offspring produced.

In deer, median birth date was 15 May, but reproductive status was determined through intensive observations in autumn to establish if marked females had fawns. We divided annual reproductive status in three categories: (1) 'no offspring weaned', (2) 'one offspring weaned', and (3) 'two or three offspring weaned'. Triplets accounted for only about 2% of litters. Since not all female deer were resighted each year ($\approx 85\%$; Gaillard *et al.* 2000), we only used females for which we had data for at least 50% of potential annual breeding attempts over the life span (Gaillard *et al.* 2000). We estimated missing data from a generalized linear mixed model, including female age and year of reproduction, as well as female identity as a random factor. This approach led to estimates very close ($R^2 = 0.93$) to those obtained using a recent capture–mark–recapture method developed for dealing with uncertain states (Rouan *et al.* 2008). Since our method predicted reproductive status values between 0 and 3, we considered females with a value between 0 and 0.5 to have weaned no offspring, between 0.5 and 1.5 to have weaned one offspring, and above 1.5 to have weaned at least two offspring. Similar to goats and sheep, analyses comparing only females that weaned at least one offspring (categories 2 and 3 combined) with females that did not wean any offspring provided similar or better fit than models with three reproductive categories ($\Delta\text{QICu} \geq 1$). We thus only present results using two reproductive states, that is, at least one offspring weaned vs. no offspring weaned. The data sets consisted of 205 female-years in goats, 1027 in sheep, and 476 in deer.

INDIVIDUAL QUALITY

To assess the influence of individual quality on the probability of reproduction, we used an index that describes heterogeneity among individuals, which we developed in a previous study. For goats and sheep, we performed a principal component analysis (PCA) on individual characteristics and life-history traits, including longevity, age at first reproduction, age at last reproduction, adult mass, offspring sex ratio, social rank (goats only), average parturition date (goats only), and average moult date (goats only). The PCA allowed

us to differentiate females based on their most influential characteristics (Table 1). We used the scores of the most influential PCA axes (the first two axes in goats and the first one in sheep; see Table 1), as determined by visual assessment of rapid decrease in consecutive eigenvalues (Cattell 1966). For roe deer, because only longevity and body mass were available, we performed an orthogonal regression between these two variables and used the scores of the regression as an index of female quality. This approach is similar to conducting a PCA with two variables and using the scores of the first axis. The scores of the regression and those of each PCA axis described heterogeneity among individuals (hereafter called 'HI scores') and provided a gradient of individual quality, with positive values representing higher-quality females and negative values lower-quality females (Table 1).

ANNUAL VARIATIONS IN RESOURCE AVAILABILITY

Because our data sets spanned several years, we accounted for yearly variations in resource availability. For goats, we used the sum of normalized difference vegetation index values (NDVI; Tucker *et al.* 2005) for June, with high NDVI representing early springs. NDVI data, however, are only available since 1982 and hence were not available for all years for sheep and deer. Instead, we used the average mass of yearling females, in September for sheep (at about 15 months of age) and in January–February for deer (at about 9 months), which has been shown to be a reliable index of yearly resource availability in populations of large herbivores (in bighorn sheep; Festa-Bianchet *et al.* 2004, and in moose; Adams & Pekins 1995). Average yearling mass was not available for all years in goats.

STATISTICAL ANALYSES

We performed logistic regressions to assess the influence of previous reproductive status, heterogeneity in individual quality, and possible interactions on the probability of (i) giving birth and (ii) giving birth and weaning an offspring (hereafter called 'probability of weaning') the following year. For parturient females, we also assessed the influence of the same variables on (iii) the probability that their offspring would survive to weaning (hereafter called 'probability of offspring survival'). For roe deer, reproductive status of females was only available at weaning. We therefore only assessed the probability of weaning at least one offspring in roe deer. Nevertheless, the probability of giving birth in this population is close to 1 for most females (between 2 years and 12 years of age; Gaillard *et al.* 1998), so the probability of weaning is likely to be similar to the probability of offspring survival.

We performed logistic regressions using generalized estimating equations (GEE) to control for repeated observations on the same individuals and avoid pseudo-replication. Because GEE are not based on maximum likelihood estimation, the Akaike information criterion (AIC) cannot be used for model selection. We therefore computed the quasi-likelihood information criterion (QICu) developed by Pan (2001). Similar to AIC (Burnham & Anderson 2002), we computed the ΔQICu and QICu weights to select the most parsimonious model. We considered models with $\Delta\text{QICu} \leq 2$ to be equivalent. When models were equivalent, we considered the model with fewest parameters as the best one, but also presented potential effects of other variables included in equivalent models. We defined a set of a priori models for each species (Supplementary Tables S1 to S3). As a surrogate of year quality, we included the covariate 'NDVI' for goats and 'average yearling mass' for sheep and deer in all models. We included population density in some models. Because population density and average yearling mass were correlated ($0.40 < r < 0.82$) in sheep and deer, we did not include both variables in the same

models. We included age as a categorical variable in all models. For goats and sheep, we modelled age in three categories: young (often primiparous), prime-aged, and old females [respectively 4–6, 7–9, and ≥ 10 years in goats (Côté & Festa-Bianchet 2001b; Festa-Bianchet *et al.* 2003) and 2–4, 5–7, and ≥ 8 years in sheep (Festa-Bianchet *et al.* 2003)]. In deer, we also considered three age classes: prime-aged (≤ 7 years old), senescent (8 to 12 years old; Festa-Bianchet *et al.* 2003), and old senescent females (13 years and older). We did not include a younger age class for deer because exploration of data revealed no difference in the probability of reproduction among females aged 2 to 7 years. We included an older age class because the probability of giving birth declined sharply in old senescent female deer (Gaillard *et al.* 2003; see Results). Although sample size was low for old senescent females ($n = 11$ female-years from seven females), models including only two age classes (prime-aged and senescent) had a poorer fit ($\Delta\text{QICu} \geq 5$) compared with models including three classes (prime-aged, senescent, and old senescent). Furthermore, models including an interaction between age and individual quality did not provide a better fit ($\Delta\text{QICu} > 2$), except for the probability of weaning in goats where they provided a similar fit ($\Delta\text{QICu} < 2$). Although models including this interaction were equivalent, they were less parsimonious (i.e. they included two additional parameters) and the interaction was not significant. We therefore presented models including only an additive effect of age.

To assess model performance, we calculated the percentage of correct predictions by comparing observed outcome (e.g. reproduced vs. did not reproduce) with expected probability for each reproductive episode. We classified a prediction as correct if the outcome was 0 and the probability was below 50% or if the outcome was 1 and the

probability was above 50%. We also presented odd-ratios (with 95% confidence intervals), a measure of effect size used in logistic regression. It is the ratio of the odds of an event occurring in one group to the odds of it occurring in another group, that is, $[p/(1-p)]/[q/(1-q)]$, where p and q represent the probabilities of each event (Littell, Stroup & Freund 2002). An odd-ratio of 1 indicates that the event is equally probable in both groups. When the odd-ratio moves towards 0, the event is less likely to occur in the first group, whereas when it moves towards infinity, the event is more likely to occur in the first group. For age effects, we always presented odd-ratios using the estimate for prime-aged females as a reference. For continuous variables, odd-ratios are the odds of an event occurring with an increase of one unit of the variable (e.g. the ratio of the odds of an event occurring when mass equals 30 kg to the odds of it occurring when it equals 31 kg). We performed all analyses in SAS (Littell *et al.* 2002) and present results as means \pm SE.

Results

MOUNTAIN GOATS

The best models describing the probability of giving birth and the probability of weaning an offspring the following year in mountain goats (Table S1) achieved 76% and 64% correct predictions, respectively. The same variables influenced the probabilities of giving birth and of weaning an offspring the following year (Table 2). The probabilities of giving birth and of weaning an offspring varied according to the interaction

Table 2. Effects of the variables included in the selected models (see Tables S1 to S3) for the probability of giving birth and the probability of giving birth and weaning an offspring, in mountain goats (Caw Ridge, Alberta, 1988–2006), bighorn sheep (Ram Mountain, Alberta, 1975–2006), and roe deer (Trois-Fontaines, France, 1975–2006)

Species	Variables	Probability of giving birth			Probability of weaning		
		d.f.	Wald χ^2	<i>P</i> values	d.f.	Wald χ^2	<i>P</i> values
Mountain goat	Included in the best model						
	NDVI	1	2.4	0.1	1	0.02	0.9
	Age	2	26.6	< 0.001	2	20.4	< 0.001
	Status	1	2.5	0.1	1	2.7	0.1
	HI-1	1	52.9	< 0.001	1	14.9	< 0.001
	Status*HI-1	1	7.1	0.008	1	8.3	0.004
Bighorn sheep	Included in equivalent models						
	Density	1	0.2	0.7	1	0.5	0.5
Roe deer	Included in the best model						
	Ymass	1	12.6	< 0.001	1	45.0	< 0.001
	Age	2	31.3	< 0.001	2	42.6	< 0.001
	Status	1	41.3	< 0.001	1	5.5	0.02
	HI	1	11.1	< 0.001	1	1.9	0.2
	Status*HI	1	15.0	< 0.001	1	10.7	0.001
Roe deer	Included in equivalent models						
	Density				1	7.3	0.007
	Age				2	36.8	< 0.001
	Status				1	1.5	0.2
	HI				1	8.3	0.004
	Status*HI				1	0.4	0.6

NDVI = normalized difference vegetation index; ymass = average yearling mass; density = population density; age = female age; status = female reproductive status the previous year in two categories: no offspring versus one offspring produced (in goats and sheep), and no offspring versus at least one offspring weaned (in deer); HI-1 = individual quality index associated with differences in mass and social rank (see Table 1); HI = individual quality index associated with differences in longevity and body mass (sheep and deer), as well as success in the last breeding opportunity (sheep only; see Table 1).

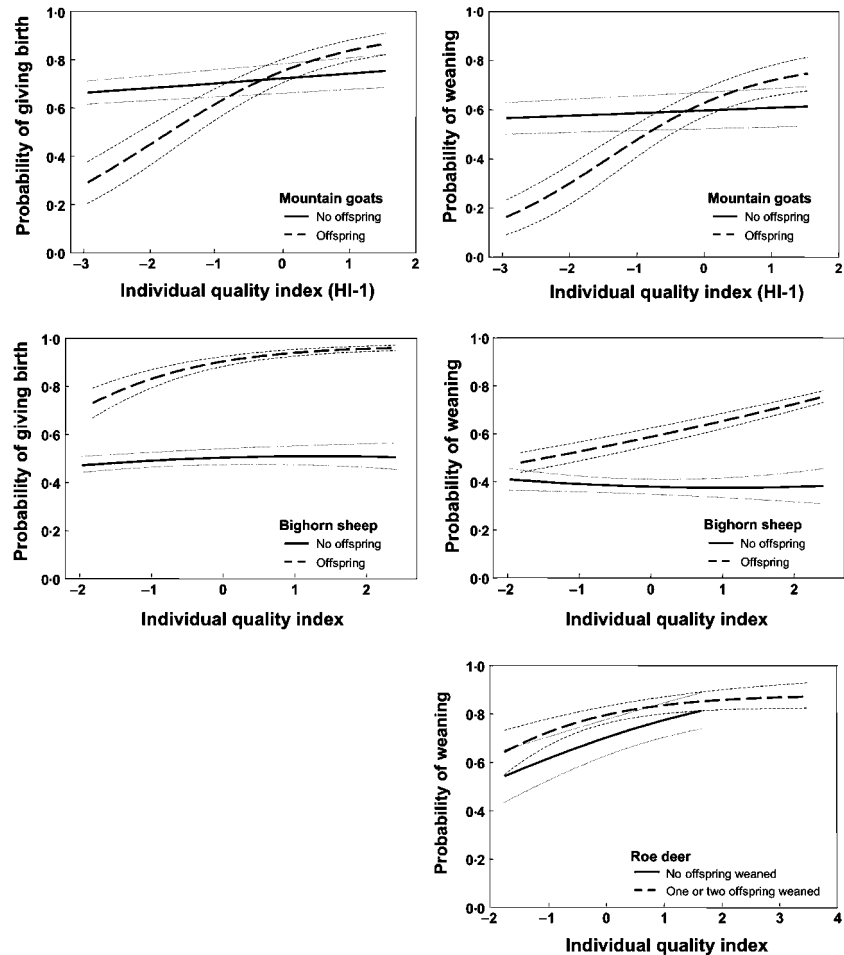


Fig. 1. Probability (logistic model predictions \pm SE) of giving birth and of giving birth and weaning an offspring according to heterogeneity in individual quality and reproductive status of females the previous year, in mountain goats (Caw Ridge, Alberta, 1988–2006), bighorn sheep (Ram Mountain, Alberta, 1975–2006), and roe deer (Trois-Fontaines, France, 1975–2006). Individual quality index in goats (HI-1) was associated with differences in mass and social rank. Individual quality index in sheep was associated with differences in longevity, body mass, and success in the last breeding opportunity. Individual quality index in deer was associated with differences in longevity and body mass (see Table 1).

between previous reproductive status and the individual quality index associated with differences in mass and social rank (HI-1; Table 2). For females that did not reproduce the previous year, the probabilities of giving birth and of weaning an offspring varied little with individual quality. For females that produced an offspring the previous year, however, both probabilities increased with quality scores (Table 2; Fig. 1). Thus, low-quality females experienced a cost of reproduction, whereas high-quality females did not (Fig. 1). Furthermore, compared with prime-aged females, the probabilities of giving birth and of weaning an offspring were about four times less likely for young females and three times more likely for old females [probability of giving birth: 4 to 6 years old: $\beta = -1.44 \pm 0.39$, odd-ratio (95% CI) = 0.24 (0.11; 0.51); 10 years and older: $\beta = 1.04 \pm 0.40$, odd-ratio (95% CI) = 2.83 (1.30; 6.18); probability of weaning: 4 to 6 years old: $\beta = -1.10 \pm 0.46$, odd-ratio (95% CI) = 0.33 (0.14; 0.83); 10 years and older: $\beta = 1.19 \pm 0.48$, odd-ratio (95% CI) = 3.28 (1.27; 8.44); Table 2]. Although reproduction apparently decreased in females aged 13 years and older, sample size was too low to model it.

For females that gave birth, several models provided equally suitable descriptions of the probability of offspring survival to weaning (Table S1). The only variable from equivalent models that appeared to influence the probability

of offspring survival was female quality associated with longevity, success in the last breeding attempt, body mass, and social rank (HI-2; Table 3). High-quality females, which lived longer, succeeded in their last breeding attempt, and tended to be heavy and dominant (high HI-2 scores; Table 1), enjoyed higher offspring survival than low-quality females (Fig. 2A). This model (#17, Table S1) achieved 82% correct predictions.

BIGHORN SHEEP

The best models describing the probabilities of giving birth and of weaning an offspring the following year in bighorn ewes (Table S2) achieved 82% and 67% correct predictions, respectively. Similar to mountain goats, the same variables influenced the probabilities of giving birth and of weaning an offspring (Table 2). Females that reproduced the previous year were much more likely to give birth and to wean an offspring than females that did not reproduce the previous year (Table 2; Fig. 1). High-quality females (i.e. with high HI scores, associated with longevity and success in the last breeding attempt; Table 1) were more likely to give birth and to wean an offspring the following year than low-quality females, but only for females that produced an offspring the previous year (Table 2; Fig. 1). Furthermore, the probabilities of giving

Table 3. Effects of the variables included in the selected models (see Tables S1 and S2) for the probability of offspring survival to weaning in mountain goats (Caw Ridge, Alberta, 1988–2006) and bighorn sheep (Ram Mountain, Alberta, 1975–2006)

Species	Variables	d.f.	Wald χ^2	P values
Mountain goat	Included in the best model			
	NDVI	1	0.8	0.4
	Age	2	2.3	0.3
	Included in equivalent models			
	HI-1	1	2.1	0.1
	HI-2	1	5.9	0.02
Bighorn sheep	Included in the best model			
	Ymass	1	32.8	< 0.001
	Age	2	9.1	0.01
	Status	1	4.7	0.03
	Included in equivalent models			
	HI	1	0.1	0.8
	Status*HI	1	5.5	0.02

NDVI = normalized difference vegetation index; ymass = average yearling mass; density = population density; age = female age; status = female reproductive status the previous year in two categories: no offspring versus one offspring produced; HI-1 = individual quality index associated with differences in mass and social rank (see Table 1); HI and HI-2 = individual quality index associated mainly with differences in longevity, body mass, and success in the last breeding opportunity (see Table 1).

birth and of weaning an offspring increased with average yearling mass [giving birth: $\beta = 0.09 \pm 0.02$, odd-ratio (95% CI) = 1.08 (1.04; 1.14); weaning: $\beta = 0.12 \pm 0.02$, odd-ratio (95% CI) = 1.12 (1.09; 1.17); Table 2]. Young and senescent females were respectively about five and three times less likely to give birth than prime-aged females [2 to 4 years old: $\beta = -1.58 \pm 0.28$, odd-ratio (95% CI) = 0.21 (0.12; 0.36); 8 years and older: $\beta = -0.95 \pm 0.36$, odd-ratio (95% CI) = 0.39 (0.19; 0.79); Table 2]. The probability of weaning was respectively three and two times less likely for young and old females than for prime-aged females [2 to 4 years old: $\beta = -1.14 \pm 0.17$, odd-ratio (95% CI) = 0.32 (0.23; 0.45); 8 years and older: $\beta = -0.59 \pm 0.19$, odd-ratio (95% CI) = 0.56 (0.38; 0.80); Table 2].

For parous ewes, the best model describing lamb survival to weaning (Table S2) achieved 71% correct predictions. The probability of offspring survival was lower for females that reproduced the previous year than for females that did not, but only for low-quality females (Table 3; Fig. 2B). For high-quality females, lamb survival was independent of previous reproductive status (Fig. 2B). Although the slopes between individual quality and lamb survival seemed positive for females that reproduced the previous year and negative for females that did not (Fig. 2B), neither differed from zero [no lamb the previous year: $\beta = -0.25 \pm 0.19$, odd-ratio (95% CI) = 0.77 (0.53; 1.12), $\chi^2 = 1.8$, $P = 0.2$, $n = 159$; lamb the previous year: $\beta = 0.20 \pm 0.11$, odd-ratio (95% CI) = 1.22 (0.98; 1.50), $\chi^2 = 3.3$, $P = 0.07$, $n = 655$]. Lamb survival increased with average yearling mass [$\beta = 0.14 \pm 0.02$,

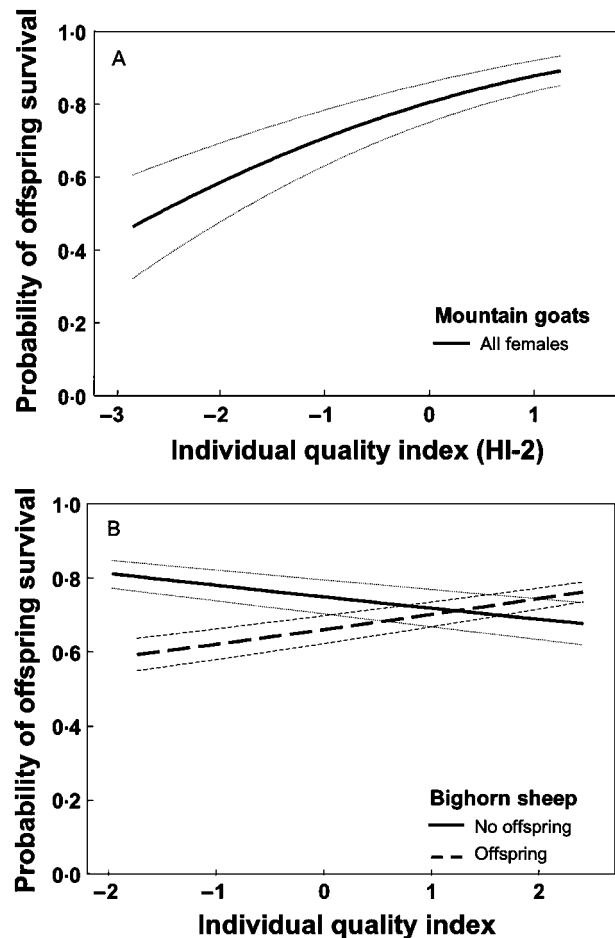


Fig. 2. Probability (logistic model predictions \pm SE) of offspring survival according to heterogeneity in individual quality (A, B) and reproductive status of females the previous year (B), in mountain goats (Caw Ridge, Alberta, 1988–2006) and bighorn sheep (Ram Mountain, Alberta, 1975–2006). Both individual quality indices were associated with differences in longevity, body mass, and success in the last breeding opportunity (see Table 1). Because the probability of offspring survival was similar for females that produced an offspring the previous year and females that did not in mountain goats, we only present the probability curve including both states.

odd-ratio (95% CI) = 1.15 (1.09; 1.20); Table 3]. Young females produced lambs that were about twice less likely to survive than either prime-aged or senescent females, but offspring survival was similar for prime-aged and senescent females [2 to 4 years old: $\beta = -0.67 \pm 0.22$, odd-ratio (95% CI) = 0.51 (0.33; 0.79); 8 years and older: $\beta = -0.23 \pm 0.19$, odd-ratio (95% CI) = 0.80 (0.55; 1.15); Table 3].

ROE DEER

The best model describing the probability of weaning an offspring the following year in female roe deer (Table S3) achieved 80% correct predictions. The probability of weaning an offspring was similar for females that had weaned at least one offspring the previous year and for those that had not (Table 2; Fig. 1). High-quality females, which were long-lived and heavy (high HI scores; Table 1), were more likely to wean

an offspring the following year than low-quality females (Table 2; Fig. 1). Unlike the results for goats and sheep, high-quality female deer had greater weaning success regardless of previous reproductive status (Fig. 1). The probability of weaning an offspring the following year tended to decrease slightly with increasing density [$\beta = -0.006 \pm 0.006$, odd-ratio (95% CI) = 0.994 (0.989; 0.998); Table 2], and was about 3 and 20 times less likely for senescent and old senescent females, respectively, than for prime-aged females [8 to 12 years old: $\beta = -1.21 \pm 0.28$, odd-ratio (95% CI) = 0.30 (0.17; 0.52); 13 years and older: $\beta = -3.38 \pm 0.59$, odd-ratio (95% CI) = 0.05 (0.02; 0.15); Table 2].

Discussion

The quantification of the long-term costs of reproduction is fundamental to our understanding of the evolution of reproductive tactics. The cost-benefit approach to reproduction, which was first introduced by Williams (1966) and then elaborated by many others (e.g. Gadgil & Bossert 1970; Bell 1980; Stearns 1992), identified costs of reproduction in many taxa (e.g. Pomeroy *et al.* 1999; Bonnet *et al.* 2002; Goodman 2006). Other studies, however, found no evidence of reproductive costs (e.g. Boyd *et al.* 1995; Toïgo *et al.* 2002; Vorburger 2005; Weladji *et al.* 2008). Variations in individual quality may explain these contradictory results, since high-quality individuals may better cope with the costs of reproduction than low-quality individuals. Here we tested the hypothesis that individual quality influences the probability of detecting a cost of reproduction in terms of future reproduction. Overall, mountain goat females had a similar probability of producing an offspring if they had reproduced or not the previous year, suggesting no cost of reproduction. After accounting for individual quality, however, we detected a cost of reproduction that was masked by individual variations. Low-quality females had a lower probability of reproduction if they reproduced the previous year than if they did not. In bighorn sheep, offspring survival was reduced by previous reproduction only for low-quality females, suggesting that the cost of reproduction was negatively correlated with individual quality (Festa-Bianchet *et al.* 1998). The probabilities of reproduction and of offspring survival to weaning increased with maternal quality in all species, suggesting greater costs of reproduction for low- than for high-quality females. Our results therefore revealed differential costs of reproduction among individuals varying in quality, and hence provide strong support to the individual quality hypothesis, as suggested in other recent studies (Cam *et al.* 2002; Beauplet *et al.* 2006; Moyes *et al.* 2006; Weladji *et al.* 2008).

In all species, high-quality females, which were generally heavy, long-lived, and succeeded in their last breeding attempt, had lower costs of reproduction or were better able to support these costs than low-quality females. Body mass can represent the overall condition of individuals and is commonly used to index individual quality. It is often positively related to female reproduction, such as age at primiparity, twinning rate, and parturition date, as well as offspring mass,

growth rate and survival (Jorgenson *et al.* 1993; Bérubé, Festa-Bianchet & Jorgenson 1996; Clutton-Brock *et al.* 1996; Pomeroy *et al.* 1999; Keech *et al.* 2000; Côté & Festa-Bianchet 2001b). There seems to be a threshold in body mass that females must reach to reproduce, and they may take reproductive pauses when their body reserves are insufficient (Doughty & Shine 1997; Pomeroy *et al.* 1999; Stewart *et al.* 2005). Reproductive pauses are common in ungulates: the probability of future reproduction averaged between 0.60 and 0.85 (irrespective of individual quality) in the sheep and goat populations, similar to that reported in other similar-sized ungulates [Cameron 1994 in caribou (*Rangifer tarandus* Linnaeus), Testa 2004 in moose, Tavecchia *et al.* 2005 in Soay sheep, Moyes *et al.* 2006 in red deer (*Cervus elaphus* Linnaeus), Weladji *et al.* 2008 in reindeer (*Rangifer tarandus* Linnaeus)]. Here we found differential costs of reproduction among females varying in asymptotic mass, suggesting that heavier females had more body reserves that they could use to compensate for the costs of reproduction than females with lower adult body mass, reinforcing the need to use body mass as a covariate to control for variation in individual quality in life-history studies.

Some long-term studies have shown that individuals living to old ages were often of higher quality than short-lived ones (Bérubé *et al.* 1999; Gaillard *et al.* 2000; Cam *et al.* 2002; Beauplet *et al.* 2006). In reindeer for example, Weladji *et al.* (2006) found that long-lived females had higher reproductive success at all ages and were particularly successful in their last breeding attempt compared with short-lived females. We also found that long-lived female goats and sheep that were successful in their last breeding attempt had lower costs of reproduction than short-lived females that failed in their last breeding opportunity. Our study therefore provides further support that longevity is correlated with individual quality in long-lived species.

Dominant mountain goats had lower costs of reproduction than subordinates. Data on social dominance were not available for bighorn sheep and roe deer. The lower costs of reproduction in dominant female goats could result from variations in food exploitation, because subordinates often have restricted access to food resources and/or forage less efficiently than dominants (Barrette & Vandal 1986; Thouless 1990). Dominance often increases reproductive success (Clutton-Brock, Albon & Guinness 1984; Côté & Festa-Bianchet 2001b), but differential costs of reproduction according to dominance status have seldom been reported in wild mammals (Gomendio *et al.* 1990). Although defending food patches during summer may be difficult for generalist herbivores, the reduced availability of resources in winter may create defensible food sources. For instance, Kojola (1997) reported higher take-over frequency of foraging craters in winter for dominant than for subordinate female caribou, which reduced mass loss in dominants compared with subordinates. In mountain goats, little is known about winter foraging in relation to dominance, but winter food resources are most likely localized and a high social rank may allow greater access to scarce vegetation patches (Masteller & Bailey 1988).

Dominant female goats may lose less mass over winter than subordinates, potentially allowing them to allocate more resources to reproduction than subordinates.

We demonstrated fundamental costs of reproduction for some individuals after accounting for heterogeneity in individual quality. Nevertheless, high-quality females appeared to avoid reproductive costs of reproduction. For example, roe deer that weaned at least one offspring showed no reduction in the probability of weaning an offspring the following year compared with females that did not wean any offspring. Possibly, individuals incurred a cost of reproduction in another unmeasured life-history trait (Shutler *et al.* 2006). This possibility is partly supported by our results for sheep, where previously breeding females had a higher probability of reproduction than previously nonbreeding females, but they had a lower probability that their new offspring would survive. However, previous reproductive status did not influence offspring survival in high-quality ewes. Alternatively, individuals that appear to suffer no cost of reproduction may be able to recover the energetic costs of reproduction and therefore avoid a fitness cost (Tuomi *et al.* 1983; Bonnet *et al.* 2002).

Costs of reproduction may only be evident at low resource availability. Some studies only reported costs of reproduction during difficult years, because individuals could regain the resources used for reproduction in favourable environments (Tuomi *et al.* 1983; Clutton-Brock *et al.* 1996; Toigo *et al.* 2002; Török *et al.* 2004). In our study, the probability of reproduction was reduced during unfavourable years in both sheep and deer. The probability of reproducing for bighorn ewes increased with average yearling mass. Average yearling mass in this population has been shown to reflect yearly variations in resource availability (Festa-Bianchet *et al.* 2004). In deer, increases in density led to a slight reduction in the probability of weaning an offspring. Even when accounting for annual variations in density and resource availability, however, some females still performed better than others.

Some females are better than others in acquiring and/or directing energy into reproduction, owing to their higher genetic or physiological quality. Van Noordwijk & de Jong (1986) demonstrated that if some genotypes were better than others at acquiring resources, some individuals should have more resources to allocate to various life-history traits, leading to positive correlations among traits (Reznick, Nunney & Tessier 2000; Vorburger 2005). Although we could not determine the exact causes of the persistent positive correlations observed, our results indicate that certain individuals supported the energetic costs of reproduction better than others. This illustrates the need to account for heterogeneity in individual quality in studies of life-history evolution to improve current theories on reproductive tactics and parental investment.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Model selection for the reproduction of mountain goat females

Table S2. Model selection for the reproduction of bighorn sheep females

Table S3. Model selection for the reproduction of roe deer females

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