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Maternal characteristics and environment affect the costs of reproduction in female mountain goats

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Abstract. Reproduction should reduce resources available for somatic investment and result in fundamental trade-offs among life-history traits. Using 18 years of longitudinal data from marked mountain goats (*Oreamnos americanus*), we assessed whether reproductive status affected female survival and future reproduction when accounting for parity, age, individual quality, population density, and environmental conditions. Reproduction reduced the probability of parturition and offspring survival in the following year. Female survival, however, was independent of previous reproduction, suggesting that females favored their own survival over that of their offspring. The lower probability of parturition in females that had a kid the previous year was only detected at high population density and among young and prime-aged females, suggesting that fitness costs of reproduction can be masked by variations in resource availability and individual characteristics. Primiparous females were less likely than multiparous females to reproduce in the subsequent year. Offspring survival was reduced at high density and after severe winters. Environmental conditions mainly influenced offspring survival, whereas female survival and fecundity were principally modulated by female characteristics. Our study highlights how different intrinsic and environmental factors can affect the probability of future reproduction and also underlines the value of long-term monitoring of known individuals.

Key words: costs of reproduction; density; environmental conditions; mountain goat; North Pacific Index; Oreamnos americanus; *reproductive strategy; survival; ungulates.*

INTRODUCTION

Because animals face limits on the time and energy available for reproduction, life-history theory predicts that iteroparous individuals should optimally allocate resources among life-history traits, principally growth, reproduction, and survival, over their lifetime (Williams 1966, Stearns 1992). In female mammals, reproduction involves high energy expenditures (Oftedal 1984). Females provide maternal care, defined as any behavior likely to increase offspring fitness, such as milk provisioning and vigilance. If maternal care leads to a fitness cost for the mother, then care is also considered a maternal investment (Clutton-Brock 1991), involving trade-offs between current reproduction and other life-history traits (Stearns 1992). These fundamental compromises, called costs of reproduction, play a key role in the evolution of reproductive strategies (Roff 2002).

In long-lived iteroparous vertebrates, survival is the main determinant of female fitness, as reproductive opportunities are usually limited to one per year (Clutton-Brock 1988, Newton 1989), and juvenile survival is often low and variable from year to year (Gaillard et al. 2000). Consequently, females in long-lived species usually favor their own survival over that of their offspring (birds: Sæther et al. 1993; mammals: Festa-Bianchet and Jorgenson 1998, Therrien et al. 2007), and survival costs of reproduction are rarely observed (Beauplet et al. 2006, Shutler et al. 2006, Le Bohec et al. 2007). Reproduction, however, often reduces the probability of reproducing in the following breeding season (Gustafsson and Sutherland 1988, Boyd et al. 1995, Yurewicz and Wilbur 2004, Le Bohec et al. 2007) or the survival of subsequent offspring (Bérubé et al. 1996, Festa-Bianchet et al. 1998). In capital breeders, whose reproductive success depends mainly on body reserves rather than on environmental conditions (Stephens et al. 2009), these costs usually occur because reproduction lowers maternal body condition (mammals: Pomeroy et al. 1999; birds: Golet et al. 1998; reptiles: Doughty and Shine 1997, Bonnet et al. 2002). Investment in current reproduction could also affect body growth. In species with determinate growth, this trade-off is mainly observed in young females that reproduce before reaching asymptotic mass, and hence bear the energetic costs of growth and reproduction at the same time (Sæther and Haagenrud 1985, Green and Rothstein 1991, Hamel and Côté 2009).

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Because heterogeneity in both individual reproductive potential and environmental conditions can mask the cost of reproduction (Cam et al. 2002), a number of individual-level and environmental variables must be considered in the examination of reproductive costs. The strength of trade-offs among life-history traits can vary drastically with environmental conditions (Persson 1995, Tavecchia et al. 2005, Townsend and Anderson 2007), because they can affect the amount of resources available for reproduction (Clutton-Brock et al. 1996, Toïgo et al. 2002, Török et al. 2004). For large herbivores in temperate and boreal environments, unfavorable weather in winter while females are pregnant can also reduce body reserves before lactation (Skogland 1983, Cameron et al. 1993, Rödel et al. 2005).

Costs of reproduction can vary substantially among mothers, because of offspring sex or mass (Gomendio et al. 1990, Kojola 1998), female age, previous breeding experience, and quality (McNamara and Houston 1996, Olsson and van der Jeugd 2002, Barbraud and Weimerskirch 2005, Hamel et al. 2009*a*). Sons generally require greater maternal care than daughters (Clutton-Brock et al. 1982, Festa-Bianchet et al. 1994*a*), possibly leading to greater costs of reproduction for females that produce sons rather than daughters (Bérubé et al. 1996). According to the terminal investment hypothesis, reproductive effort should increase with age as residual reproductive value declines (Pianka and Parker 1975, Clutton-Brock 1984). Young females that reproduce before completing body growth may also suffer greater costs of reproduction than prime-aged females that have reached asymptotic mass (Bonenfant et al. 2003, Descamps et al. 2009). Finally, high-quality females may show lower costs of reproduction than low-quality females (Gomendio et al. 1990, Cam et al. 2002, Hamel et al. 2009*a*). Individual quality can be defined as a covariation among life-history traits at the individual scale, resulting in heterogeneity among individual performances within a population (Hamel et al. 2009*b*).

We used 18 years of longitudinal data to assess the short-term costs of reproduction in female mountain goats (*Oreamnos americanus*). Mountain goats are a good model species in which to study the costs of reproduction. Females are capital breeders that lose ~30% of their mass during winter (Festa-Bianchet and Côté 2008). They must therefore accumulate sufficient body reserves during a very short growing season to reproduce successfully in the following year. Their unexpectedly low annual reproductive rate (~75%) suggests that reproduction is costly (Festa-Bianchet and Côté 2008). Finally, although they reach asymptotic mass at 6 or 7 years, most females start reproducing at 4 or 5 years and must simultaneously allocate resources to somatic growth and reproduction. As a result, young reproducing females have a lower summer mass gain than non-reproducing and older females (Hamel and Côté 2009), possibly leading to age-related differences in costs of reproduction.

We examined how reproduction in one year affected the probability that, in the following year, a female would (a) survive, (b) give birth, (c) wean an offspring, and (d) produce an offspring that will survive the winter. We tested whether these probabilities varied with breeding experience, age, sex of previous offspring, density, and environmental conditions. Because the covariation of asymptotic mass and social dominance affects costs of reproduction in mountain goats (Hamel et al. 2009*a*), we also included this variable in the analyses. We expected that breeding in the previous year would reduce a female's probability of reproduction (b) and the survival of subsequent offspring (c, d), but not its own survival (a). We also expected to find greater costs for young, growing females than for prime-aged females, and predicted that senescent and low-quality females would suffer greater costs of reproduction than prime-aged and high-quality females. We did not expect population density to affect costs of reproduction, because very few density-dependent effects have been observed in this population, despite its doubling in size over 20 years (Festa-Bianchet and Côté 2008). We expected costs of reproduction to increase following severe winters during pregnancy, or poor environmental conditions at parturition.

METHODS

Study area and population

We studied mountain goats on Caw Ridge (54° N, 119° W), west-central Alberta, Canada. Goats use 28 km^2 of alpine tundra and subalpine open forest at 1750–2170 m elevation. The climate is subarctic–arctic and snowfall can occur during any month. The main goat predators are grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) (Festa-Bianchet and Côté 2008). We used longitudinal data from marked females between 1990 and 2007. Total population size in June increased from 81 in 1990 to 159 in 2004, and then stabilized at ~155 individuals (Festa-Bianchet and Côté 2008). We captured goats in salt-baited traps and chemically immobilized them (Haviernick et al. 1998). We marked individuals with plastic ear tags and collars. Since 1993, 98% of goats aged 1 year and older were marked. We aged adult goats not marked as juveniles by counting their horn annuli, a technique reliable up to 7 years of age (Stevens and Houston 1989). We weighed captured goats with a spring scale (±0.5 kg) and recorded mass (± 0.5 kg) of adult females using three remotely controlled electronic platform scales (50 × 130 cm) baited with salt. Further descriptions of capture techniques are in Côté et al. (1998).

Reproductive success

From mid-May to late September 1990–2007, we observed the behavior of adult females and their offspring daily using spotting scopes (15–45×). We evaluated the annual reproductive status of each female from observations of nursing behavior. A few days prior to parturition, female goats usually isolate themselves to give birth to a single offspring. During the birth season (mid-May to early June), we intensively searched the study area each day to record parturitions. Although some females may have given birth and lost their offspring before we noted the presence of a kid, this is unlikely to be common because we have very few observations of females never seen with a kid but seen in isolation or showing signs of having given birth when captured. We determined the annual survival of females and their offspring by their presence in the study area during the following summer. We never documented emigration by adult females or kids, and no female or kid missing in one year was ever seen again in the study area (Festa-Bianchet and Côté 2008). Because most kids were unmarked, we determined the identity of kids that survived to one year from observations of yearling–mother associations in spring (Gendreau et al. 2005) and DNA analyses (Mainguy 2008). We determined the sex of most kids by urination posture and by observations of the vulvar patch in females (Festa-Bianchet and Côté 2008). Our data set included 555 female-years from 87 females.

Individual quality

Differences in female reproductive potential can mask the costs of reproduction (Reznick et al. 2000, Hamel et al. 2009*a*). We previously used principal component analyses (PCA) to identify two covariations among life-history traits as indexes of individual quality that influenced female lifetime reproductive success (Hamel et al. 2009*a, b*). The first covariation, which explained the greatest heterogeneity among females, included asymptotic mass and social rank, whereas the second included mainly longevity and success in the last breeding attempt, as well as asymptotic mass and social rank. Heavy and dominant females had greater reproductive success (Hamel et al. 2009*b*) and were more likely to reproduce in consecutive years (Hamel et al. 2009*a*) than light and subordinate females. Because social rank and asymptotic mass are important individual characteristics influencing reproduction in this species, we included in our analyses the average adult rank and asymptotic mass of adult females, providing an index of quality independent of age. Social rank and mass were not available for all female-years, but correlations between annual and average rank and mass were very high (rank: $r = 0.74$, $P < 0.001$, $n = 374$; mass: $r = 0.69$, $P < 0.001$, $n = 211$). Using annual values rather than averages on a reduced data set led to similar results.

We determined the social rank of females from observations of agonistic interactions. Observations were evenly distributed among individuals over the summer. During each encounter, we recorded the identity of the initiator, winner, and loser. We considered an encounter to be resolved when one of the opponents withdrew. For each dyad, we considered an individual to be dominant if it won more than 50% of the interactions with the other individual (Côté 2000). We recorded 15,830 interactions (48 ± 24 interactions per female per year, mean ± SD) and observed a mean (± SD) of 51% ± 9% of dyads per year. Dominance relationships were significantly linear for all years (all h' values ≥ 0.2, all P values < 0.001), and thus we ordered adult females in annual hierarchies according to de Vries (1998) using Matman 1.0 for Windows (Noldus Information Technology 1998). Because age is highly correlated with rank ($r > 0.9$; Côté 2000), we calculated age-specific social ranks as the residuals of the regression of rank on age. We used the average of all age-specific ranks available from each female between 4 and 12 years of age as her social rank.

To determine asymptotic mass, we adjusted body mass measurements to 15 July, using the average rates of summer mass gain for five age classes (3, 4, 5, 6, and $\geq$7 years old; see Festa-Bianchet et al. 1996). We then adjusted all available mass measurements for each female to age 7 (when females reach asymptotic mass; see Festa-Bianchet and Côté 2008), using linear mixed models (Littell et al. 2006) with "year" and "female identity" as random effects to account for repeated measures, and "reproductive status" and "age" as covariates. Finally, we performed an orthogonal regression between average asymptotic mass and age-specific social rank and used the values of the regression as an index of individual quality (Hamel et al. 2009*b*). This procedure is similar to performing a PCA and using the scores of the first component (Legendre and Legendre 1998). Because the relationship between adult mass and social rank was positive ($r = 0.27$), high values of the orthogonal regression represented heavy and dominant individuals.

Annual variations in resource availability and environmental conditions

To account for yearly variations in resource availability in spring/summer, we used the Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2005), specifically the sum of the bimonthly NDVI values for June. In our study area, high NDVI values represent early spring green-up (Hamel et al. 2009*c*). We used the November–March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994) to represent environmental conditions during winter. At Caw Ridge, winters with high NPI values are colder and snowier than winters with low NPI values (Hamel et al. 2009*b*). We used NPI values to measure winter severity during gestation and NDVI values to measure environmental conditions at parturition. We did not use local weather data because they contained numerous missing values.

Statistical analyses

We initially classified annual reproductive status in four categories: (1) females that showed no signs of having given birth, (2) females whose kid died before late September, (3) females whose kid survived to late September but died before the following May, and (4) females whose kid survived to the following May. Analyses comparing all females that reproduced (categories 2–4) with females that did not reproduce, however, provided a much better fit (Quasi-likelihood Information Criterion $\Delta QIC_u \geq 4$; Pan 2001) than analyses using four categories. Results from models including two or four reproductive categories were similar. Therefore, we only present results comparing previously breeding and previously nonbreeding females.

We used logistic regressions to assess the influence of female reproductive status (breeding or nonbreeding); age (three classes: young (3–6 years; incomplete body growth), prime-aged (7–9 years; completed growth and stable survival), and old (10 years and older; survival senescence)); female quality; kid sex; population density (total population in June, as a continuous variable); winter severity during pregnancy (NPI); environmental conditions at parturition (NDVI); and possible interactions on the probability that, in the following year, a female would:

(1) survive to May, hereafter called "probability of survival"; (2) give birth, hereafter called "probability of parturition"; (3) wean her offspring, hereafter called "probability of offspring survival over summer"; and (4) produce an offspring that will survive from weaning to one year, hereafter called "probability of offspring survival over winter."

We used Generalized Estimating Equations (GEE) with compound symmetry as the covariance structure (i.e., constant variance and covariance) to control for the correlation between repeated measurements of the same individual, assuming equal correlation among all within-group errors related to the same group (Littell et al. 2002). 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 (QIC_u; Pan 2001). Similarly to AIC (Burnham and Anderson 2002), we used ΔQIC_u and QIC_u weights to select the best model, and presented effects included in the best model based on 95% confidence intervals (CI) of odds ratios and Wald statistics. We considered models with $\Delta QIC_u \leq 2$ to be equivalent. Based on parsimony, we selected the model with fewer parameters when models were equivalent, but we also present 95% CI of odds ratios for other variables included in competing models. We defined a priori a set of models for each analysis (see Appendix: Tables A1–A4). Instead of including "year" as a random effect in all models to account for yearly variations, we included NDVI and NPI, which are more ecologically relevant than simply "year." Because models with missing values are not comparable and we did not know the sex of all kids, we analyzed a reduced data set to compare models with and without this variable. For all four probabilities mentioned, however, the complete and the reduced data set resulted in the same model selection, suggesting no influence of "kid sex" on any probability. We therefore present only results using the complete data set.

To assess the performance of selected models, we reported values for the area under the receiver operating characteristic curve (AUC) and calculated the percentage of correct predictions for each reproductive episode (Fielding and Bell 1997). We classified a prediction as correct if the observation was 0 and its predicted probability was below 50%, or if the observation was 1 and the prediction was 50% or more. We also present odds ratios (with 95% confidence intervals), a measure of effect size in logistic regression (Littell et al. 2002). For age effects, we always present odds ratios using the estimate for senescent females as a reference.

We also compared the four probabilities between primiparous and multiparous females. Because almost all primiparae were aged between 3 and 6 years (only two were 7-year-olds), models with both primiparity and age did not converge. Therefore, we tested the influence of primiparity on a data set including only young females. For each probability, we used the model selected from the complete data set, added "primiparity," and reran the models for young females only. We then compared QIC_u of the initial model with that including primiparity and presented Wald statistics for this variable. We performed all analyses in SAS (version 9.1.3; Littell et al. 2002) and present results as means ± SE based on robust estimates.

Results

Probability of survival

The best model for female survival (#33; Appendix: Table A1) achieved 91% correct predictions (AUC = 77%). Only age influenced the probability of female survival (Table 1). Old females had lower survival (0.80 ± 0.04) than both young (0.99 ± 0.01) and prime-aged (0.96 ± 0.02) females (young vs. old: odds ratio = 22.7; 95% CI [5.6–92.6]; prime-aged vs. old: odds ratio = 6.3 [2.9–13.9]). Although previous reproductive status was included in an equivalent model, previously breeding and nonbreeding females had similar survival probabilities (0.91 ± 0.02; Appendix: Table A1). All CIs of odds ratio for other variables included in equivalent models included 1.0 (quality = [0.79–1.18]; quality × age: young vs. old = [0.83–3.00], prime-aged vs. old = [0.95–2.89]; density = [0.98–1.02]; Appendix: Table A1).

Probability of parturition

The best model for the probability that a female will give birth in the following year (#13; Appendix: Table A2) achieved 71% correct predictions (AUC = 66%). Overall, females that did and did not breed in the previous year had a similar probability of parturition, but there was a cost of reproduction for young females (status × age interaction) and for all females at high population density (status × density interaction; Table 1,

TABLE 1. Influences of environmental conditions and female characteristics in the previous year on probabilities of female survival, parturition, and offspring survival over summer or winter in mountain goats (*Oreamnos americanus*) at Caw Ridge, Alberta, Canada (1990–2007).

Dependent variable, with variables in best model	df	Wald χ^2	P
Probability of adult female survival			
NPI	1	0.9	0.3
NDVI	1	2.0	0.2
Age	2	39.2	<0.001
Probability of parturition			
NPI	1	1.2	0.3
NDVI	1	0.0	1.0
Status	1	2.3	0.1
Density	1	0.6	0.5
Age	2	5.1	0.08
Status × Density	1	4.3	0.04
Status × Age	2	13.7	0.001
Probability of offspring survival over summer			
NPI	1	5.1	0.02
NDVI	1	4.8	0.03
Density	1	6.9	0.009
Probability of offspring survival over winter			
NPI	1	18.5	<0.001
NDVI	1	3.5	0.06
Status	1	3.7	0.05
Mother quality	1	0.5	0.5
NPI × Mother quality	1	12.6	<0.001

Notes: NPI is the North Pacific Index in the current year. NDVI is the Normalized Difference Vegetation Index in the current year. Age is female age in the previous year, by category: young (3–6 years), prime-aged (7–9 years), and old (10 years and older). Status is reproductive status in the previous year by category: breeding vs. nonbreeding females. Density is the total population density in the previous year. Mother quality is an index of female quality, with high values representing individuals with high body mass and social rank.

Appendix: Table A2). In young females, the probability of parturition was much lower for previously breeding than for previously nonbreeding females (Fig. 1A). The difference declined as females aged, and it disappeared for older females (Fig. 1A). The probability of parturition for previously breeding and nonbreeding females was similar at low population density (Fig. 1B). At high density, however, the probability of parturition was 25% lower for previously breeding than for previously nonbreeding females (Fig. 1B). All CIs of odds ratio for other variables included in equivalent models included 1.0 (quality = [0.96–1.62]; quality × status = [0.44–1.05]; Appendix: Table A2).

Offspring survival over summer

For parturient females, the best model describing offspring survival over summer (#27; Appendix: Table A3) achieved 80% correct predictions (AUC = 65%). The probability of weaning an offspring was only influenced by environmental conditions (Table 1, Appendix: Table A3). Cold and snowy winters, with high NPI values during pregnancy, reduced the probability of weaning (odds ratio = 0.81; 95% CI [0.67–0.97]). In addition, the probability that females would wean their offspring was lower when spring was early (high June NDVI), than when it was late (odds ratio = 0.07 [0.01–0.76]). Offspring summer survival decreased with increasing density (odds ratio = 0.98 [0.97–0.99]). It was ~10% lower when population size was at 155 compared with 85 individuals. CIs of odds ratios for other variables included in equivalent models all included 1.0 (quality = [0.74–1.25]; quality × status = [0.54–2.16]; Appendix: Table A3).

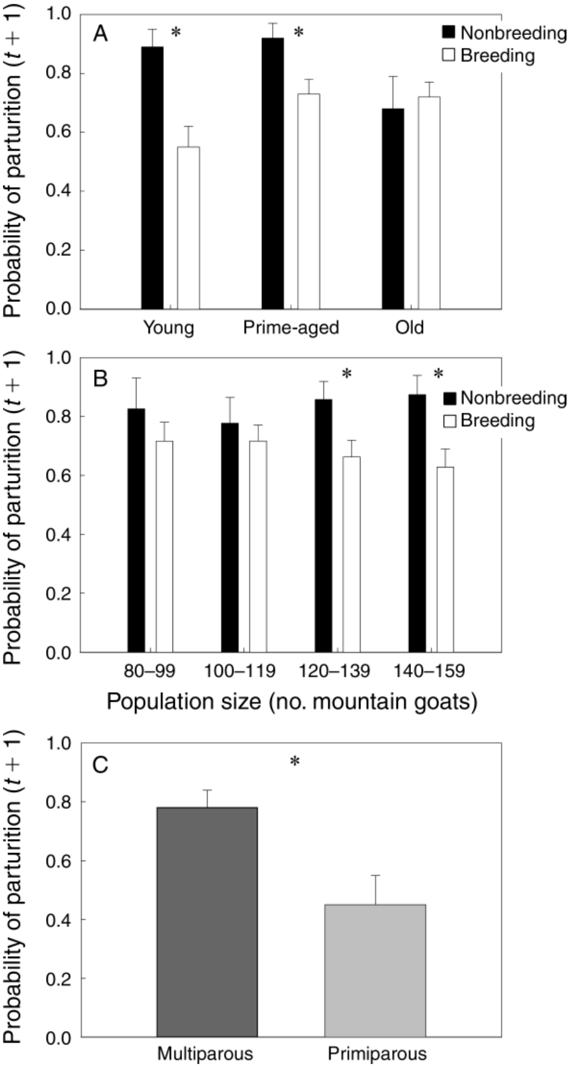

FIG. 1. Probability of parturition (mean + SE) of mountain goats (*Oreamnos americanus*) at Caw Ridge, Alberta, Canada (1990–2007), according to (A) female reproductive status and age (young, 3–6 years; prime-aged, 7–9 years; old, 10 years and older) in the previous year; (B) female reproductive status and population size in the previous year; and (C) female primiparity. Significant differences ($P < 0.05$) are indicated by asterisks.

Offspring survival over winter

For females that weaned an offspring, the best model describing the probability of kid survival over winter (#39; Appendix: Table A4) achieved 81% correct predictions (AUC = 70%). Unlike summer survival, winter survival was affected by both environmental conditions and maternal characteristics (Table 1, Appendix: Table A4). Offspring of previously nonbreeding females were about 2.5 times more likely to survive over winter than offspring of previously breeding females (odds ratio = 2.5; 95% CI [1.00–6.16]). Similarly to survival over summer, cold and snowy winters (high NPI values) during gestation reduced the probability of first-winter survival (odds ratio = 0.71 [0.60–0.83]). This effect, however, was observed mainly in low-quality females (NPI estimate for females of above-average quality: odds ratio = 0.88 [0.73–1.04]; NPI estimate for low-quality females: odds ratio = 0.54 [0.40–0.73]; Table 1, Appendix: Table A4). Kid winter survival was not affected by NPI values in that winter ($\chi^2 = 2.2$, df = 1, $P = 0.13$), and models including this variable had $\Delta\text{QIC}_\text{u} > 8$ compared with those including NPI in the winter before birth. In contrast with their effect on summer survival, early springs (high NDVI values) tended to have a positive influence on kid survival over winter (odds ratio = 9.8 [1.0–96.0]). Female age was also included in an equivalent model, but CIs of odds ratios included 1.0 (young vs. old = [0.85–3.74]; prime-aged vs. old = [0.98–4.05]; Appendix: Table A4).

The influence of primiparity

The probability of parturition was 4.5 times greater for multiparous females than for those that were primiparous in the previous year ($\Delta\text{QIC}_\text{u}$ [model including primiparity – model excluding it, using a reduced data set] = −17.9; $\chi^2 = 21.5$, df = 1, $P < 0.001$; Fig. 1C). Primiparity did not reduce survival: 69 of 70 primiparous females survived to the following year. Primiparity did not influence weaning success ($\Delta\text{QIC}_\text{u} = 1.3$; $\chi^2 = 1.0$, df = 1, $P = 0.3$) or offspring survival to one year ($\Delta\text{QIC}_\text{u} = 0.8$; $\chi^2 = 1.3$, df = 1, $P = 0.3$).

DISCUSSION

Female mountain goats adopted a conservative reproductive strategy, favoring their own survival over investment in current offspring. Reproduction did not reduce female survival, but it decreased both the probability of future parturition and the survival of future offspring. Breeding experience reduced the costs of reproduction, because the probability of future parturition was greater for multiparous than primiparous females. Unexpectedly, however, older females had lower costs than younger females and our measure of quality did not influence reproductive costs. We did not expect density to influence the costs of reproduction, because few density-dependent effects had been observed in this population. Once previous reproduction was accounted for, however, density reduced the probability of parturition and of offspring survival over summer. Poor environmental conditions decreased kid survival, but did not influence the probability that a female would survive or give birth.

Probability of female survival

Reproduction did not affect survival in female mountain goats. We also previously reported a positive association between age at first reproduction and longevity (Hamel et al. 2009*b*). Similar to our results, most studies of large mammals found that reproduction did not affect female survival (Festa-Bianchet et al. 1998, Packer et al. 1998, Testa 2004, Beauplet et al. 2006, Lake et al. 2008, Weladji et al. 2008). Survival costs of reproduction, however, have been reported in two ungulate populations (Tavecchia et al. 2005, Moyes et al. 2006) and are also occasionally reported in other long-lived species (Boyd et al. 1995, Golet et al. 1998), but we currently do not have an explanation for these differences.

Reproduction should affect survival if individuals face a trade-off between maintenance and current reproduction. In long-lived vertebrates, however, females prioritize their own mass gain over the development and survival of their young when resources are limited, and hence favor their survival above that of their offspring (Sæther et al. 1993, Festa-Bianchet and Jorgenson 1998, Therrien et al. 2007). In contrast, survival costs of reproduction are frequently reported in short-lived species (e.g., Nilsson and Svensson 1996, Koivula et al. 2003), where individuals have few reproductive opportunities during their lifetime. Consequently, they seldom skip reproduction and may allocate more energy to reproduction than to survival, compared with long-lived individuals. Trade-offs between survival and reproduction have also been reported in reptiles, where gravidity decreases survival through higher predation risk (Shine 1980, Madsen 1987). Although predation risk associated with high mass has also been reported in birds (Gosler et al. 1995), gestation does not appear to impose survival costs in mammals (Clutton-Brock et al. 1989).

Probability of future reproduction

Investment in current reproduction reduced the probability of future parturition in female goats, as reported in other species (Testa 2004, Le Bohec et al. 2007). Females may be either physiologically incapable of reproducing following high energetic investment in previous reproduction, or selected not to reproduce in consecutive years to avoid survival costs. One interesting aspect of our study is that this reproductive cost occurred only at high density, as reported in red deer (*Cervus elaphus*; Clutton-Brock et al. 1983). At low population density, resources may allow females to compensate for the energetic costs of reproduction before the next reproductive episode. Furthermore, females also had lower weaning success if population density in the previous year was high than if it was low (see also Festa-Bianchet et al. 1998), suggesting that density-dependent effects on female condition prior to parturition may persist during summer. Density dependence first affected juvenile survival and subsequent reproduction of breeding females, supporting the suggestion of Stephens et al. (2009) that capital breeders should show delayed density dependence because they rely on body reserves accumulated over long periods. They also provide further evidence that mountain goat females adopt a conservative reproductive strategy, linking the order of density-dependent demographic changes predicted by population dynamics theory (Eberhardt 2002) to female reproductive strategy: when density first increases, females reduce reproductive effort in favor of their own condition, so that the negative effects of density appear in young of the year before they affect other population parameters (Festa-Bianchet and Côté 2008).

We previously showed that individual quality, measured by social rank and mass, increased the probability of parturition in previously breeding, but not in previously nonbreeding, female goats (Hamel et al. 2009*a*). The interaction between female quality and previous reproductive status, however, was not as important in the present study (Appendix: Table A2). Because our previous analysis required data on lifetime reproductive success for entire cohorts, it included mainly females that lived during the first years of the study, at low density. When we restricted the analysis presented here to years with low density, we obtained a significant interaction between female quality and previous reproductive status on the probability of parturition ($\chi^2 = 3.8$, df $= 1$, $P = 0.05$). These results illustrate that when resources were limited all females paid a cost of reproduction, but at low density only low-quality females experienced a cost. High-quality females seem better able to meet the energetic requirements for reproduction in consecutive years than do low-quality females, but only when conditions are favorable.

The costs of reproduction were lower for both older and multiparous females than for younger and primiparous females. According to the terminal investment hypothesis (Pianka and Parker 1975), residual reproductive value should decline as females age and reproductive investment should increase (e.g., Clutton-Brock 1984, Descamps et al. 2007). Many species, however, do not conform to this expectation, as older mothers can increase reproductive effort compared with younger mothers without suffering greater costs (Green 1990, Cameron et al. 2000). Instead, they seem able to better target their investment. Female goats also showed lower costs of reproduction as they aged. Because older female goats reach higher social rank (Côté 2000), they may have access to greater food resources than younger, subordinate females. Females also attain adult size a few years after starting to reproduce (Festa-Bianchet and Côté 2008), so that older females are larger and may have greater stored reserves than younger females. Furthermore, with age, females may reduce the costs of reproduction through a better allocation of resources to maintenance and reproduction.

In long-lived species, young females often bear the high energetic costs of growth and lactation simultaneously, resulting in a fundamental trade-off between mass gain and reproduction (Green and Rothstein 1991, Bonenfant et al. 2003). Primiparous mountain goats have a daily summer mass gain ~20% lower than nonbreeding females of the same age (Hamel and Côté 2009), possibly explaining the costs of reproduction seen in primiparous females. This trade-off between growth and reproduction is probably less influential in short-lived capital breeders, where reduced growth following reproduction does not reduce lifetime reproductive success (Bonnet et al. 2002).

Offspring survival

Although female survival and reproductive rate were generally not affected by environmental conditions, offspring survival over summer and over the first winter declined if the winter preceding birth was cold and snowy, and this effect was more important for low-quality (low mass and subordinate rank) than high-quality females. We suggest that harsh winters affect juvenile survival partly through effects on the resource allocation strategy of females during pregnancy and lactation. Females may spend more energy in thermoregulation and locomotion when winters are cold and snowy than when conditions are more favorable, possibly lowering their body condition (Rödel et al. 2005). Pregnant females may thus allocate less energy to the fetus in severe winters compared with favorable ones, potentially leading to a lower birth mass (Forchhammer et al. 2001), a major determinant of juvenile survival (Keech et al. 2000, Moyes et al. 2006). Furthermore, females with reduced reserves following harsh winters appear to allocate energy obtained from nutritious spring forage to replenish their reserves rather than to milk production (Gaillard et al. 2000, Bardsen et al. 2008). Therefore, lower body reserves in spring may also affect lactation in capital breeders. Although very few studies have directly addressed these questions, food-restricted red deer females were found to have lower body mass, produce less milk and of poorer quality, and have calves with lower body growth than did control females (Landete-Castillejos et al. 2003).

Better foraging conditions in early spring could benefit offspring directly, as well as indirectly, by providing more energy to mothers during the first weeks of lactation. As expected, early springs improved offspring survival over the first winter but, surprisingly, reduced survival over summer. The opposite influence of spring conditions on offspring survival over winter and summer might result from viability selection: in years of low summer survival, only high-quality offspring may survive, potentially leading to higher winter survival. Viability selection, however, does not explain the counterintuitive result of lower summer survival following early springs. Predation can have a strong impact on survival of newborns (Testa 2004), as suggested in mountain goats (Festa-Bianchet et al. 1994*b*), and predation pressure may be stronger in early than in late springs. For instance, bears emerge sooner from dens in early than in late springs (Schooley et al. 1994), and early snowmelt may allow predators greater access to goat habitat during the first weeks after birth, when offspring are most vulnerable to predation.

Selection should favor the reproductive strategies providing the greatest fitness. Here, we have shown that female mountain goats adopt a conservative reproductive strategy, because current reproduction affects future reproduction, but not maternal survival. This conservative strategy probably evolved because fitness of female goats is mainly determined by survival (Festa-Bianchet and Côté 2008), as in other long-lived species (Clutton-Brock 1988, Newton 1989). One noteworthy aspect of our study is that costs of reproduction were not apparent in old females and at low density. This demonstrates that the occurrence of reproductive costs is highly variable and dependent on both individual state and environmental conditions, emphasizing the importance of accounting for these variables when studying costs of reproduction. Furthermore, female survival and reproduction were principally modulated by female attributes, whereas environmental conditions mainly influenced the probability of offspring survival, showing that the influence of these variables can vary among traits. Because costs of reproduction play a key role in the evolution of reproductive strategies, knowledge about the way in which costs of reproduction vary according to individual state and environmental conditions provides clues to how selective pressures may also differ over time. Our study suggests that a variety of selective pressures influence the evolution of reproductive strategies, and reinforces the value of longitudinal studies as an enhanced framework for studying life-history trade-offs.

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APPENDIX

Model selection for the probability of female survival and parturition, and for the probability of offspring survival over summer and winter (*Ecological Archives* E091-140-A1).