# Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal

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When resources are limited, current maternal investment should reduce subsequent reproductive success or survival. We used longitudinal data on marked mountain goats *Oreamnos americanus* to assess if offspring mass at weaning affected maternal survival and future reproduction. Offspring mass was positively correlated with survival of old mothers, suggesting that mothers produced lighter kids, and hence reduced reproductive effort, in their last reproduction. Offspring mass at weaning did not affect survival of young and prime-aged mothers, but females that had weaned heavy offspring had a reduced probability of subsequent reproduction in years of low population density. Because offspring survival is correlated with weaning mass, mothers' allocation to reproduction involves a tradeoff between current and future fitness returns. We demonstrate for the first time that allocation to current offspring mass in an iteroparous mammal reduces the probability of subsequent reproduction.

Williams (1966) suggested that limited resource availability should result in negative co-variations among fitness components. Because reproduction has high energetic requirements (Robbins 1993), allocation to current reproduction should involve a tradeoff with future reproduction or survival (Stearns 1992, Roff 2002). To assess the fitness costs of reproduction, one must therefore measure how current reproductive effort affects future reproduction and survival (Hamel et al. 2010a).

Because the tactics of energy allocation to reproduction vary among species, different measures of reproductive effort have been used. In short-lived species, individuals seldom skip reproduction and often produce many offspring at each of few reproductive attempts (Speakman 2008). Current reproductive effort is often measured as the number of offspring produced (e.g. mammals: Descamps et al. 2009, birds: Shutler et al. 2006, insects: Creighton et al. 2009) and sometimes as total offspring mass (Huber et al. 1999). In contrast, long-lived species tend to adopt a conservative reproductive tactic, because greater longevity generally increases fitness (Clutton-Brock 1988). They may skip reproductive opportunities to favour their own survival and often produce a single offspring at a time (Gaillard et al. 1989). Current reproductive effort is thus most often described as a binary variable: breeding versus non-breeding. This classification, however, cannot determine whether or not variation in resource allocation to each offspring affects residual parental fitness. Instead, measures such as offspring mass are required to quantify reproductive allocation in these species. Because offspring mass is difficult to measure in wild animals, few studies of long-lived species have used it to assess costs of reproduction (Clutton-Brock et al. 1983, Festa-Bianchet and Jorgenson 1998).

When assessing reproductive allocation in wild mammals, one must account for variables known or suspected to affect reproductive strategies. The state of an individual (determined by its body condition, age, and current resource availability; McNamara and Houston 1996) could modify patterns of resource allocation. The terminal investment hypothesis predicts that reproductive effort should increase with age because residual reproductive value declines (Pianka and Parker 1975, Clutton-Brock 1984). Therefore, older individuals should invest more in reproduction, and thus show higher costs of reproduction, compared with younger ones. Furthermore, individual variability in resource acquisition and allocation results in heterogeneity in reproductive potential that can mask costs of reproduction (van Noordwijk and de Jong 1986). For instance, individuals that acquire more resources could make a greater allocation to reproduction without incurring greater fitness costs compared with low-quality individuals (Doughty and Shine 1997, Hamel et al. 2009a).

Here, we used longitudinal data from individually marked mountain goats *Oreamnos americanus* to assess if offspring mass affected maternal survival and future reproduction. Previously, we showed that female mountain goats that reproduced one year had a lower probability of future reproduction than females that did not reproduce, but mainly at high density and among young females (Hamel et al. 2010b). Survival, however, was similar for breeders and non-breeders, in agreement with the conservative reproductive tactic of this long-lived species (Hamel et al. 2010b). That study addressed

the influence of current reproduction per se on future fitness, assessing current reproductive effort as a binary variable and hence comparing future fitness of females that allocated to current reproduction (breeders) with females that did not (non-breeders). That study, however, did not test whether mothers allocating more to current reproduction, for example by producing a heavier offspring, suffered reduced future fitness compared with mothers allocating less. Here, we address this specific question by evaluating whether offspring mass affects subsequent reproduction and survival of mountain goat mothers. Using a high-quality dataset, we demonstrate for the first time that allocation to current offspring mass in an iteroparous mammal affects fitness costs of reproduction of mothers.

## Material and methods

### Study area and population

We studied mountain goats at Caw Ridge (54°N, 119°W), west-central Alberta, Canada. Goats use 28 km² 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 collected from marked females between 1990 and 2009 (see Festa-Bianchet and Côté 2008 and Hamel et al. 2010b for more details). Total population size in June increased from 81 in 1990 to 159 in 2004, and then remained between 150 and 165 individuals. We captured goats in traps and marked them with plastic ear tags and collars. Since 1993, 98% of goats aged one year and older were marked. We aged adult goats not marked as juveniles by counting their horn annuli, a technique reliable up to seven years of age. We weighed captured goats with a spring scale (±0.5 kg) and recorded mass of adult females and their kids using three remotely-controlled electronic platform scales (±0.5 kg; 50 × 130 cm) baited with salt (Festa-Bianchet and Côté 2008).

### Reproduction and survival

From mid-May to late September 1990–2009, we observed goats almost daily using spotting scopes. We evaluated the annual reproductive status of each female from observations of nursing behaviour. A few days prior to parturition, females usually isolate themselves to give birth to a single offspring. We determined birthdates either by direct observations of births or by daily observations of presence/absence of a kid for each female. In some cases, we estimated kid birthdates within five days from the characteristics of the umbilical cord, and by comparing the kid's behaviour and body size with those of known-age kids. We determined the sex of most kids by urination posture and by observations of the vulvar patch in females (Festa-Bianchet and Côté 2008). We determined the annual survival of females by their presence in the study area during the following summer (1 June). We never documented emigration by adult females, and no adult female missed one year was ever sighted in subsequent years (Festa-Bianchet and Côté 2008). For females that reached

three years of age, longevity averaged nine years, ranging from three to 18 years, and lifetime reproductive success averaged four, ranging from 0 to 10 offspring produced.

### Offspring mass

Kid mass was recorded throughout the summer and adjusted to 1 September using sex-specific regression equations of mass gain over time (see Festa-Bianchet et al. 1996 for a detailed example). Kid mass on 1 September was strongly negatively correlated with birth date (r = –0.62, n = 124, p < 0.001). To control for birth date, we calculated age-specific kid mass using the residuals of the regression of mass on birth date. Thus, positive/negative values of residual mass represented kids that were heavier/lighter for their age in September, which we assumed to reflect variation in maternal allocation. We used residuals rather than including birth date as a covariate to limit the number of variables in our analyses. Nevertheless, including birth date as a covariate led to the same results, likely because parturition date did not affect the probability of survival ($\chi^2$ = 1.9, p = 0.2, DF = 1) or of future parturition ($\chi^2$ = 0.1, p = 0.9, DF = 1) of females, and did not vary with female age (r = –0.07, n = 124, p = 0.5). We rarely saw suckles in September and therefore kid mass on 1 September approximates weaning mass.

### Variations in annual conditions and individual heterogeneity

To account for yearly variations in resource availability during the growing season, we used the sum of the two normalized difference vegetation index (NDVI; Pettorelli et al. 2005) values recorded in June. In our study area, high NDVI values represent early spring green-up (Hamel et al. 2009c). We used the November–March anomalies of the North Pacific index (NPI; Trenberth and Hurrell 1994) to quantify 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. 2009b). We included NPI and NDVI as covariates to control for winter severity during gestation and for environmental conditions at parturition, respectively.

Differences in resource acquisition and allocation among individuals can mask the costs of reproduction (van Noordwijk and de Jong 1986). Therefore, we included an index of female reproductive potential as a covariate to account for heterogeneity among individuals. In mountain goats, social rank and asymptotic mass (reached at ~seven years of age) strongly influence reproduction and explain most heterogeneity observed among females (Hamel et al. 2009a, b). Thus, we performed a robust orthogonal regression between asymptotic mass and age-specific social rank and used the values of the regression as an index of individual heterogeneity, or 'quality' (as in Hamel et al. 2009a, b). This regression minimizes the orthogonal (i.e. perpendicular) distances between the data and the fitted line, in contrast with ordinary linear regression that minimizes the vertical distances. Therefore, using the values of the orthogonal regression is similar to performing a principal component analysis and using the scores of the first component. Since the relation between adult mass and social rank was positive (r = 0.3), high

values of the orthogonal regression represented heavy and dominant individuals. We used average adult rank and mass rather than annual values because social rank and body mass were not available for all female-years. Correlations between annual and average rank and mass were very high (r's > 0.7), and using annual values rather than averages on a reduced data set led to similar results.

Asymptotic mass of adult females was determined by adjusting body mass measurements to 15 July, based on age-specific regression equations describing mass gain over summer for five age classes (3, 4, 5, 6 and ≥ 7 years old, see Festa-Bianchet et al. 1996 for a detailed example). We then adjusted all available mass measurements for each female to age seven (when females reach asymptotic mass, see Festa-Bianchet and Côté 2008), using linear mixed models with 'year' and 'female identity' as random effects to account for repeated measures, and 'reproductive status' and 'age' as covariates. Social rank of females was determined from observations of agonistic interactions. For each dyad, we considered an individual dominant if it won more than 50% of the interactions with the other individual (Côté 2000). 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 annual age-specific ranks from each female between four and 12 years of age as her social rank.

## Statistical analyses

We performed logistic regressions to assess the influence of offspring mass on the probability that a female would 1) survive and 2) give birth the following year. In both models, we included NPI, NDVI, and female 'quality' as covariates to control for winter severity during pregnancy, environmental conditions at parturition, and individual heterogeneity in resource acquisition and allocation, respectively. Because population density and age influence survival and reproduction in female mountain goats (Hamel et al. 2009a, 2010b), we included these two variables in the models and assessed the influence of the following interactions: kid mass × population density and kid mass × female age. Although the sex of the kid does not influence future reproduction or survival of mothers (Hamel et al. 2010b), its interaction with kid mass could be influential. We therefore also evaluated the influence of kid sex and kid sex × kid mass. Population density was the total population size in June. Although we normally use three age classes for analyses of female goat survival and reproduction (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]; Festa-Bianchet et al. 2003), we used two and four age categories respectively for the analysis of future survival and future reproduction. Because no female aged between three and six years for which offspring mass was available died, we compared survival of females aged 3 to 9 years and 10 years and older. Survival does not differ between young and prime-aged females (Hamel et al. 2010b). To analyze future reproduction, we divided the youngest age class in two categories to account for the reduced probability of future reproduction in primiparous females (Hamel et al. 2010b). We thus used four age categories: young primiparous (3–6 years), young multiparous (4–6 years), prime-aged (7–9 years), and old (10 years and older). Our survival analysis included 124 female-years from 59 females, while the dataset for the probability of future reproduction included 115 female-years from 57 females. Analyses including offspring mass and female 'quality' as covariates produced similar results to analyses using the ratio of offspring mass to maternal mass (for 82 females for which annual mass was available); we therefore only present the former.

For each analysis, we used generalized estimating equations (GEE) with compound symmetry as the covariance structure (i.e. constant variance and covariance) to control for 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). The influence of kid mass and its interaction with mother age and population density, as well as kid sex and its interaction with kid mass, were assessed in the full model and were considered significant when p < 0.1. The same results were obtained when reducing the full model using stepwise procedures. To assess model performance, we report the area under the receiver operating characteristic curve (AUC), which measures the overall predictive accuracy of the model independent of a specific threshold (Fielding and Bell 1997). AUC values vary from 0.5 to 1, and represent the percentage of randomly drawn pairs (i.e. one of each group) that the model classifies correctly. Generally, the predictive accuracy of a model is classified as 'worthless' with an AUC of 0.5 to 0.6, 'poor' with 0.6 to 0.7, 'fair' with 0.7 to 0.8, 'good' with 0.8 to 0.9, and 'excellent' with 0.9 to 1.0. For significant variables, we present odds ratio (with 95% CI), a measure of effect size in logistic regression (Littell et al. 2002). An odds ratio is the odds of an event occurring in one group to the odds of it occurring in another group, i.e. $[p/(1 - p)]/[q/(1 - q)]$, where $p$ and $q$ represent the probabilities of each event. An odds ratio of 1 indicates that the event is equally probable in both groups. When the 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 continuous variables, an odds ratio is the odds of an event occurring with an increase of one unit (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 ± SE based on robust estimates.

## Results

After accounting for annual conditions (NPI, NDVI), mother 'quality', mother age, and population density, offspring mass was related to both survival and future reproduction of mothers (Table 1). Old mothers that weaned a light kid had much lower survival than old mothers that weaned a heavy kid (Table 1A, Fig. 1A). Survival of young and prime-aged mothers, however, was very high and unaffected by offspring mass (Table 1A, Fig. 1A). There was no influence of the

Table 1. Influence of kid mass, the sex of the kid, maternal age, and population density on the probability of future survival (A) and parturition the following year (B) of mountain goat females at Caw Ridge, Alberta, Canada (1990-2009).†

| | Odds ratio [95% CI] | DF | Wald χ² | p |
|---|---|---|---|---|
| **(A) Probability of survival of mothers** | | | | |
| Kid mass | 2.82 [1.33; 6.00] | 1 | 4.0 | 0.04 |
| Kid mass × Mother age | 0.39 [0.18; 0.86] | 1 | 4.8 | 0.03 |
| Non-significant variables: | | | | |
| Kid mass × Density | | 1 | 2.5 | 0.11 |
| Kid sex | | 1 | 0.8 | 0.4 |
| Kid sex × Kid mass | | 1 | 1.7 | 0.2 |
| **(B) Probability of future parturition of mothers** | | | | |
| Kid mass | 0.10 [0.02; 0.47] | 1 | 9.7 | 0.002 |
| Kid mass × Density | 1.014 [1.004; 1.025] | 1 | 8.5 | 0.004 |
| Non-significant variables: | | | | |
| Kid mass × Mother age | | 3 | 4.9 | 0.2 |
| Kid sex | | 1 | 0.2 | 0.6 |
| Kid sex × Kid mass | | 1 | 1.6 | 0.2 |

†North Pacific index, Normalized difference vegetation index, and mother quality were included as covariates to account for annual environmental conditions and heterogeneity in female quality. Maternal age and population density were also included as single effects in the models because they affect the probability of survival and parturition in female mountain goats (Hamel et al. 2010b). The influence of kid mass and its interaction with mother age and population density, as well kid sex and its interaction with kid mass, were then assessed in the full model and were considered significant with p < 0.1. Mother age was divided in two categories for the probability of survival and four for the probability of parturition (Material and methods). For age effects, we presented odds ratio using the estimate for females > 10 years as a reference.

interaction between offspring mass and population density on female survival, which was also independent of offspring sex or its interaction with kid mass (Table 1A). The AUC of the model describing maternal survival was 0.86, revealing good predictive accuracy.

Irrespective of age, mothers with heavy kids had a lower probability of parturition the following year than mothers with light kids, but only at low population density (Table 1B, Fig. 1B). At high density, the probability of future parturition was less than half that at low density and it was not affected by offspring mass (Table 1B, Fig. 1B). The probability of future parturition was not affected by the interaction between offspring mass and mother age, by the sex of the kid or its interaction with kid mass (Table 1B). The AUC of the model describing the probability of future parturition was 0.83, and hence this model also had a good predictive accuracy.

## Discussion

Long-lived species have usually evolved a slow life-history strategy that favours adult survival over investment in current offspring, in opposition to the fast strategy of short-lived species that promotes investment in current reproduction over adult survival (Stearns 1983, Gaillard et al. 1989, Promislow and Harvey 1990, Bielby et al. 2007). In mountain goats, we have previously shown that reproduction does not affect survival of females, but it reduces their probability of future parturition and the survival of their future offspring (Hamel et al. 2010b), thereby confirming the conservative reproductive tactic expected for this long-lived species. Our results here suggest further that mountain goats have evolved a slow rather than a fast life-history strategy, because mothers allocating more to their offspring did not suffer greater mortality than mothers allocating less, but they had a reduced probability of future reproduction.

Heavy kids enjoy greater survival to one year of age than light kids (Côté and Festa-Bianchet 2001). Offspring mass is a major determinant of offspring survival in many long-lived species (Moyes et al. 2006). Mothers of heavy offspring therefore likely received a fitness benefit which, however, reduced their residual reproductive value (sensu Williams 1966). Therefore, our results demonstrate that offspring mass measures maternal investment in mountain goats. In other long-lived mammals for which the influence of differential allocation of reproductive effort has been assessed, offspring mass did not affect the probability of future reproduction (*Cervus elaphus*; Clutton-Brock et al. 1983) or maternal survival (*Ovis canadensis*; Festa-Bianchet and Jorgenson 1998). In short-lived species, however, differential allocation of reproductive effort, which is most often measured as litter size, can influence future reproduction and survival (Iason 1990, Lambin and Yoccoz 2001). Because standardised variance in offspring mass in long-lived species is likely smaller than variance in offspring number in short-lived species, the detection of a cost of reproduction as a result of differential allocation in offspring mass in long-lived species is challenging (Hamel et al. 2010a). We present the first evidence that differential allocation to offspring mass among breeding females leads to a direct fitness cost of reproduction in an iteroparous mammal.

In many species, costs of reproduction increase when resources are limiting, such as at high density (review in mammals by Hamel et al. 2010a). For income breeders, greater costs arise mainly because individuals have fewer resources to allocate to reproduction, whereas in capital breeders costs occur principally because it takes longer to recover body condition after a reproductive event (Doughty and Shine 1997). In mountain goats, which are capital breeders, we found that the negative influence of kid mass on future reproduction was mainly seen at low density. At high density, all mothers had a similar probability of future parturition, but this probability

**(A)**

**(B)**
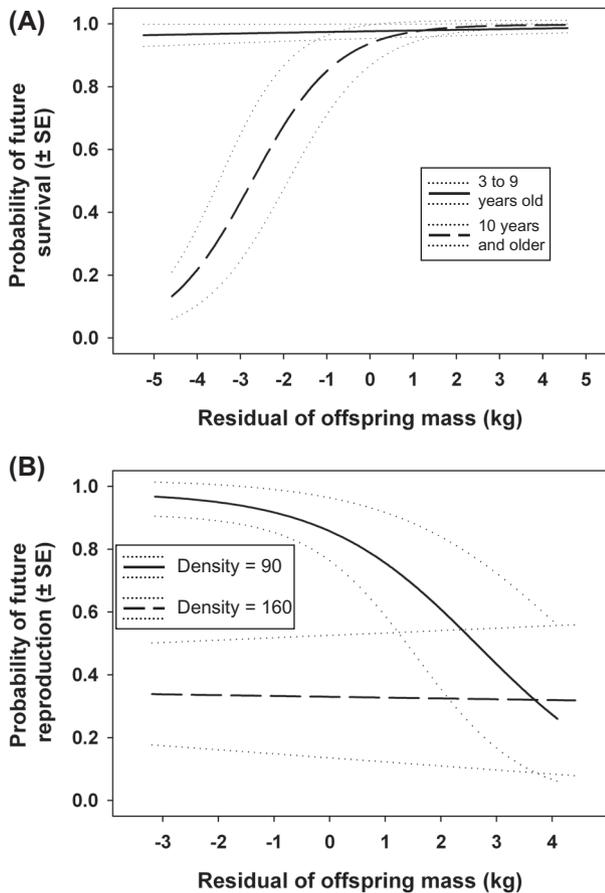
Figure 1. Probability of survival of mothers in relation to the mass of their current kid (corrected for birth date, Material and methods) and their age (A), and probability of parturition of mothers in the subsequent year in relation to the mass of their current kid (corrected for birth date) and population density (B), in mountain goats at Caw Ridge, Alberta, Canada (1990–2009). Curves represent model predictions ± SE. Although predictions are presented for population densities of 90 and 160 (B), density was analysed as a continuous variable and varied between 81 and 164 individuals.

was less than half that at low density (Fig. 1B). Female goats that reproduced have a lower probability of future parturition than non-breeding females, but only at high density (Hamel et al. 2010b). These results suggest that the costs of reproduction increase at high density, as the future reproduction of breeding females is reduced irrespective of allocation to the current offspring. In this study, we found that costs associated with high allocation to the offspring, on the other hand, are evident only at low densities. Thus, at high density, producing any offspring reduced the residual reproductive value of mothers, whereas at low density only females producing heavy offspring suffered a reduction in residual reproductive value. Better foraging conditions at lower densities probably allowed mothers that limited allocation to offspring to recover from the costs of reproduction. Variation in population density therefore should modify the life-history tactics adopted by females.

Although mountain goat mothers with heavy kids did not show a decrease in survival compared with mothers with light kids, old mothers that weaned a light kid were much

more likely to die the following year than old mothers that had weaned a heavy kid (Fig. 1A). This result is opposite to predictions of the terminal investment hypothesis (Pianka and Parker 1975). Because investment in reproduction by definition involves fitness costs (Trivers 1972), this hypothesis therefore predicts that fitness costs of reproduction should increase with age. Although this hypothesis looks a priori relatively simple, most studies investigated changes in reproductive effort with age without actually measuring costs of reproduction, and hence could not quantify terminal investment (Mysterud et al. 2005, Billing et al. 2007, Creighton et al. 2009). Reproductive effort is the proportion of energy allocated to reproduction, but it is not necessarily correlated with parental investment (Cameron et al. 2000), an allocation that entails fitness costs of current reproduction (see Hamel et al. 2010a for a review of these definitions). Hence, most previous studies only assessed terminal 'allocation' and not terminal 'investment' (see Weladji et al. 2010 for a revealing illustration of these different processes). Of the few studies that assessed terminal investment, some suggested that it likely occurred (Pärt et al. 1992, Paul et al. 1993, Hanssen 2006), while others refuted the hypothesis (Cameron et al. 2000, Festa-Bianchet and King 2007, Bouwhuis et al. 2010). Therefore, evidence for terminal investment is equivocal. Our results suggest that mountain goat females suffer from a decline in condition and reproductive performance before death, as suggested by Rattiste (2004) and Weladji et al. (2006). Offspring mass in mountain goats does not vary with female age (Côté and Festa-Bianchet 2001), but the fitness costs of reproduction decrease with age (Hamel et al. 2010b). Therefore, reproductive allocation appears relatively constant with age, whereas reproductive investment decreases. Old female goats may better target their investment than younger mothers and do not seem to conform to the terminal investment hypothesis. For terminal investment to be selected, the average reproductive value of the current offspring should at some point be greater than that of the mother. As suggested by Festa-Bianchet and King (2007), this may never happen for long-lived species where juvenile survival is low and much more variable than adult survival (Gaillard et al. 2000). More studies are clearly needed to evaluate when terminal investment should be expected and to determine if direct fitness costs of resource allocation to offspring mass also exist in other species. Because patterns of reproductive investment should respond to selection pressures, studying variations in resource allocation and investment is central to understanding evolution of life-history strategies (Roff 2002).

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