



Reproductive success in female mountain goats: the influence of age and social rank

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In mammals, reproductive success may be positively correlated with both maternal age and social rank. Because social rank often increases with age, however, the effects of rank and age on reproductive success are difficult to separate. We studied a marked population of mountain goats, *Oreamnos americanus*, to assess the relative effects of maternal age and social rank on kid production and survival. Adult females formed a linear and stable dominance hierarchy. Kid production increased with both age-specific maternal social rank and age, but decreased slightly after 9 years of age. The influence of dominance was particularly important among 3- to 5-year-old females, and the positive effect of dominance on kid production decreased with increasing female age. Age-specific social rank and maternal age did not affect kid survival to autumn or to 1 year. Kids whose mothers were heavy for their age had a higher probability of surviving to weaning and to 1 year than kids born to light females. When age was accounted for, female survival was not related to social rank. Social rank appears to be an important determinant of reproductive success for female mountain goats, especially among young females.

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Life history theory predicts that reproductive effort should increase with age as reproductive value decreases (Stearns 1992). In several iteroparous mammals, reproductive success increases with age (Reiter et al. 1981; Clutton-Brock et al. 1982; Ozoga & Verme 1986; Festa-Bianchet 1988; Sand 1996), until the onset of reproductive senescence (Lunn et al. 1994; Bérubé et al. 1999). Parental experience increases with age and can improve reproductive success (Reiter et al. 1981; Ozoga & Verme 1986; Lunn et al. 1994). Similarly, social dominance increases with age in many large mammals (Rutberg 1986; Thouless & Guinness 1986; Festa-Bianchet 1991; Locati & Lovari 1991) and may also correlate positively with reproductive success (Ellis 1995). High social rank in males often confers priority of access to mates in species where males can defend females (LeBoeuf 1974; Clutton-Brock et al. 1982; Wolff 1998). Among females, social rank has also been shown to correlate positively with reproductive success (Dunbar & Dunbar 1977; Reiter et al. 1981; Clutton-Brock et al. 1984, 1986; Cassinello & Alados 1996; Pusey et al. 1997), although not all studies have found such a relationship (Berger 1986; Festa-Bianchet 1991).

In species without paternal care, individual characteristics such as age, social rank or body mass may affect maternal investment and offspring survival (Clutton-Brock et al. 1985; Gomendio et al. 1990). Because life history theory predicts that reproductive effort and experience both increase with age (Stearns 1992), females may give more maternal care or better protect their young as they age (Reiter et al. 1981; Lunn et al. 1994; Byers 1997). Similarly, high-ranking or large females may have a greater capacity to provide maternal care (Arnbom et al. 1994; Wauters et al. 1995), thus increasing the probability of offspring survival (Clutton-Brock 1984). Alternatively, old or dominant mothers may target their investment in offspring more efficiently than young or subordinate mothers without necessarily investing more (Cameron et al. 2000). Life span explains much of the variance in female reproductive success in long-lived mammals (Clutton-Brock 1988; Byers 1997). Because high social rank often gives priority of access to food in mammals (Thouless 1990), dominant females may survive better than subordinate ones (van Noordwijk & van Schaik 1987), and therefore reproduce for a longer time.

Mountain goats, *Oreamnos americanus*, are polygynous, with pronounced sexual dimorphism: adult males are about 40% heavier than females (Côté 1999). Although their horns can injure or even kill conspecifics (Geist 1967), female mountain goats have higher rates of intraspecific aggression than any other female ungulate

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for which aggressiveness has been measured (Fournier & Festa-Bianchet 1995). In addition, females maintain a high social status up to their death (Côté 2000b), suggesting that the effects of dominance may be more important and long lasting in goats than in other ungulate species. The life history consequences of social dominance in mountain goats, however, are unknown.

Female goats in our study population form a highly linear and stable dominance hierarchy, strongly correlated with age (Côté 2000b). The stability of female social rank over time is an important element in evaluating the adaptive significance of social dominance. Because social rank within a cohort remains stable over most of the reproductive life of a female (Côté 2000b), any advantages associated with high rank would substantially increase lifetime reproductive success (Alados & Escós 1992).

Because reproductive success correlates positively with both maternal age and social rank, and because social rank often increases with age, the relative effects of age and social rank on reproductive success are often confounded (Clutton-Brock et al. 1986; Wolff 1998). In mountain goats, most of the variance in female social rank is explained by age (Côté 2000b); therefore our principal objective was to assess the relative effects of both age and social rank on female reproductive success, taking into account the effects of age on social rank. We used multiple logistic regression to test the hypothesis that kid production and survival increase with maternal age and age-specific social rank.

METHODS

We studied mountain goats on Caw Ridge (54°N, 119°W), a front range of the Rocky Mountains in west-central Alberta, Canada. Goats used about 28 km² of alpine tundra and open subalpine forest at about 2000 m altitude. The study population has not been hunted since 1969 and ranged from 76 to 133 individuals during the study.

From 1987 to 1999, we captured 225 goats in remote-controlled wooden box traps and self-tripping nylon mesh Clover traps baited with salt (Clover 1956; Côté et al. 1998). Capture dates were from 30 May to 10 October (mean 15 July). We used a long-pole syringe to immobilize adults via intramuscular injection of xylazine hydrochloride (5 mg/kg), the effect of which was later reversed by intramuscular injection of 0.7–1.2 mg of idazoxan (Haviernick et al. 1998). Immobilized goats were blindfolded and hobbled; measuring and marking took 20–40 min (Côté et al. 1998; Haviernick et al. 1998). We handled kids and most yearlings without drugs. We marked animals with canvas collars, standard Allflex plastic ear tags or radiocollars. All adult females (≥ 3 years old) were marked during this study.

For goats first caught as adults, we determined age by the number of horn annuli, a technique reliable up to 7 years of age (Brandborg 1955; Stevens & Houston 1989). The exact age was known for more than 85% of the females studied. We weighed goats to the nearest 0.5 kg with a spring scale. Very few adult females were captured after 1993 (see Ethical note below), therefore our sample size for body weight was small.

We used spotting scopes (15–45 \times) to sample goat behaviour at distances ranging from 200 to 700 m. Observations were conducted almost daily from mid-May to mid-September. For each group sighted, we noted the identity of individuals present and determined which marked females were nursing a kid. From mid-May to early June, we searched the study area intensively and attempted to find as many adult females as possible each day, to determine which ones had given birth. We measured overwinter survival by determining which individuals survived to 1 June the following year. No goat missed in one year was ever seen again on Caw Ridge, and all females were seen more than 30 times each summer.

From 1994 to 1997, we used all-occurrences sampling and focal observations (Altmann 1974) to record 2792 agonistic encounters between adult females. Average individual rate of aggressive interactions among adult female mountain goats was 3.4 interactions/h (Fournier & Festa-Bianchet 1995). Initiator, winner and loser were noted for each interaction. The outcome of most agonistic encounters was very obvious and we defined an interaction as resolved when one of the opponents withdrew (Drews 1993). For each dyad, an individual was considered dominant if it won more than 50% of interactions with the other individual (Hand 1986). We used only aggressive encounters recorded in natural conditions because those recorded at the trap site often had different outcomes (Côté 2000a).

Statistical Analyses

We ordered individuals in annual hierarchies that were most consistent with a linear hierarchy according to the method of de Vries (1995, 1998; Côté 2000b). Briefly, the dominance hierarchy was reorganized by an iterative procedure (1000 randomizations) that ranked individuals by minimizing the number and strength of inconsistencies in the matrix. An inconsistency appears in the current rank order when individual j dominates i , but j is ranked below i (de Vries 1998). The absolute difference between the ranks of two individuals involved in an inconsistency is called the strength of that inconsistency (de Vries 1999). All the procedures were implemented with Matman 1.0 for Windows (Noldus Information Technology 1998).

Because matrix size varied from 38 females in 1994 to 45 in 1997, we transformed social ranks according to the formula $1 - \text{rank}/N_i$ where N_i is the number of adult females during year i . Social ranks therefore varied from 0 (subordinate) to 1 (dominant). Because more than 94% of interactions were won by the older female (Côté 2000a, b), we used the residuals of the regression of social rank on age (thereafter age-specific social rank) in all analyses.

We used multiple logistic regression (GLM) models (McCullagh & Nelder 1989) to assess the effects of age and age-specific social ranks on kid production and kid survival to weaning and to 1 year. We used the backward stepwise procedure with the log likelihood ratio and the criteria $\alpha=0.05$ to enter and $\alpha=0.10$ to remove in SPSS 8.0 for Windows. Each kid was included only once in the data set, but each mother contributed on average 1.6 kids

(maximum four, or 2% of the data set) during the study. To account for repeated observations of females contributing more than one kid and for stochastic between-year variation, we also used generalized linear mixed models (GLMMs) to assess the effects of maternal characteristics on kid production and survival, including the random effects of year and female identity. GLMMs are a more sophisticated class of generalized linear models (McCullagh & Nelder 1989) that allow random effects to be fitted within the framework of regular logistic regression (Schall 1991). Considering the variance component of year and mother identity, however, only slightly modified the estimates of the final models because the random effects were very small. Thus, because GLMs are much simpler than GLMMs and led to very similar results, we present only the results of GLM analyses.

Means are given \pm SE, unless otherwise stated.

Ethical Note

The traps were only open overnight, from 2100–2300 hours, and were checked every 45 min in the early morning, starting at first light. If no goats came, the traps were closed at 0830–0900 hours. We used two blinds about 80 m from the traps to observe the goats and, in most cases, observers were present when goats were caught. Goats were normally (>90% of the time) processed within 1 h of being caught (maximum 4 h). Individuals in box traps could not see outside and remained very calm. Observers intervened as soon as goats in Clover traps showed any sign of stress. Animals did not suffer from heat stress because morning temperatures were very rarely above 5 °C (Côté & Festa-Bianchet 2001b). Allflex plastic ear tags were attached with special pliers provided by the company; these tags were safe and are used widely to mark domestic livestock and to study wild ungulates. Kids received the smallest Allflex tags (3 × 4.5 cm), yearlings the medium (4 × 6 cm) and other goats the large ones (6 × 7.5 cm). We also fitted 57 individuals with radiocollars weighing about 0.8% (0.5–1.0%) of total body mass (Côté et al. 1998). Canvas collars and ear tags were not removed because the study is still ongoing. However, radiocollars were removed when they stopped transmitting.

Xylazine is an effective and safe drug for immobilization of mountain goats captured in traps (Haviernick et al. 1998). Goats took 3–9 min to recover after injection of the antidote (Haviernick et al. 1998). However, chemical immobilization decreased the probability of kid production the following year by 3- and 4-year-old females, and increased the risk of kid abandonment (Côté et al. 1998). These results were surprising because no case of lamb abandonment or decrease in reproduction after using the same drug and antidote on the mother have been detected in a long-term study of bighorn sheep, *Ovis canadensis* (Jorgenson et al. 1990; Côté et al. 1998), and most cases of offspring abandonment reported in ungulates occurred within 2 weeks of birth (Livezey 1990). In our study, no kid less than 3 weeks old was captured and more than 75% of kids were captured when older than 6 weeks. After we realized the negative effects

of drugging, we immediately released all 3- and 4-year-old females, and all lactating females caught without their kid (Côté et al. 1998). From 1994 on, we avoided catching any kid or lactating female before mid-August and stopped drugging all lactating females. Starting in 1998, we did not capture any kid. For these reasons, we did not include in the analyses data for kid production for 3- and 4-year-old females the year after they had been drugged. In addition, we removed all abandoned kids from analyses of survival, because abandonment decreased kid survival (Côté & Beaudoin 1997; Côté et al. 1998). Some abandoned kids disappeared and we presume they were killed by predators (Côté et al. 1998). Survival of kids handled and tagged was not different from that of kids not captured (Côté et al. 1998). Because uncollared kids appeared more likely to survive to 1 year, although not significantly, than kids with radiocollars, we stopped fitting kids with radiocollars in 1993. Although goats in box traps were more calm than goats caught in Clover traps, the type of trap did not affect the efficiency of the drug or the risk of injury (Haviernick et al. 1998). Our results suggest that researchers must test for possible effects of handling instead of assuming that no detrimental effects occur. Long-term consequences of capture and marking could be important and should be addressed in all studies. For mountain goats, we recommend not to drug young (3- and 4-year-old) and lactating females and to limit the use of radiocollars to \geq 1-year-old individuals (Côté et al. 1998).

This research project was approved by the Animal Care Committee of the Université de Sherbrooke, affiliated with the Canadian Council for Animal Care.

RESULTS

Kid Production

Female mountain goats produced their first kid between 3 and 7 years of age, but the majority of females were primiparous when 4 or 5 years old ($\bar{X} \pm SD = 4.6 \pm 0.9$ years; number primiparous at each age: 3 years: 2; 4 years: 19; 5 years: 14; 6 years: 4; 7 years: 2). Not all female goats reproduced every year: the proportion producing a kid increased gradually up to 9 years of age (Fig. 1a). Age was positively related to kid production in a multiple logistic regression model with social rank (Table 1). The significant age² term (Table 1) indicated that the relationship between age and kid production was curvilinear, kid production first increasing, then decreasing after about 9 years (Fig. 1a). Very few 3-year-old females reproduced, but their exclusion did not modify the model.

Kid production increased with age-specific social rank (Fig. 1b). Social rank and age were strongly positively correlated: on average 88% of the variance in social rank each year was explained by age (Côté 2000b). Therefore, we used the residuals of age with social ranks in the logistic model. The residuals of the regression between social rank and age for females that produced a kid (0.012 ± 0.011 , $N=93$) were greater than those for barren females that did not (-0.013 ± 0.010 , $N=63$; $P<0.0002$ in a multiple logistic regression model, Table 1). In addition,

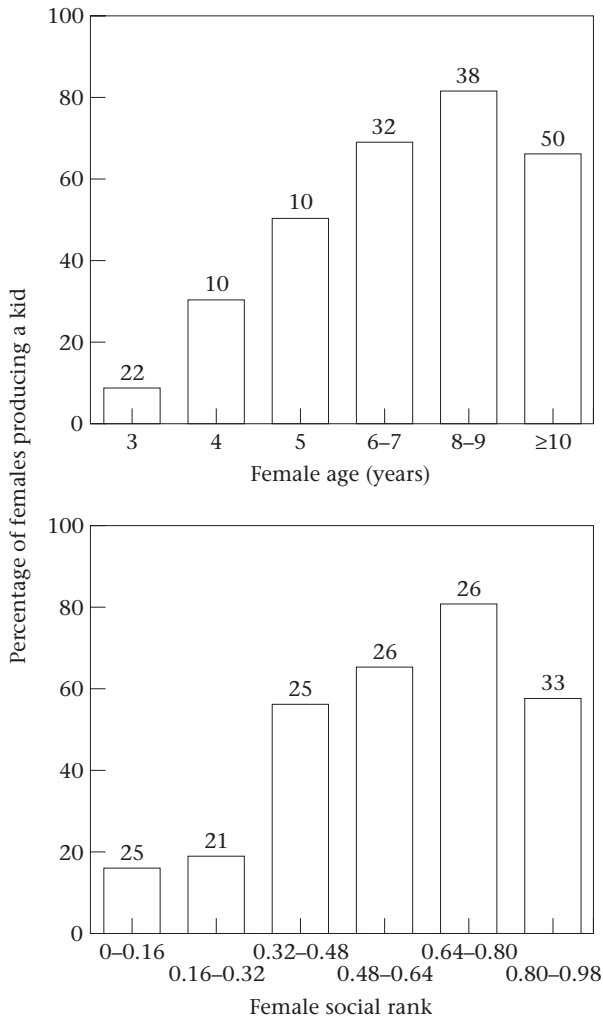


Figure 1. Kid production in relation to female (a) age and (b) social rank in mountain goats on Caw Ridge, Alberta, 1994–1997. Social ranks vary from 0 (subordinate) to 1 (dominant), sample sizes are shown above each histogram.

a negative interaction between age and age-specific social rank (Table 1) revealed that the positive effect of dominance on kid production decreased with maternal age. High social rank was mostly important for females less than 6 years old (Table 1, Fig. 2). Separate analyses for female and male kids led to similar results.

We hypothesized that dominant females would produce their first kid at a younger age than subordinate females. Age of primiparity did not vary between years (Kruskal–Wallis ANOVA: $H_5=1.8$, $P=0.8$). Thus, we pooled all years and found that social rank at 3 years of age was not related to the age of primiparity (one-way ANOVA: $F_{2,14}=0.03$, $P=0.9$).

Kid Survival

Female age did not affect the probability of kid survival to autumn (4 months; approximate physiological weaning; mean age was 8.4 ± 0.3 years for 70 females that weaned a kid, and 7.8 ± 0.4 years for 27 females that did

not; Table 1). Similarly, kid survival to 1 year was unrelated to maternal age (mean age was 7.9 ± 0.4 years for 49 females whose kid survived to 1 year, and 8.4 ± 0.4 years for 45 females whose kid died; Table 1). We did not detect any effect of age-specific social rank on kid survival to weaning (mean residuals of social rank were 0.003 ± 0.013 for 68 females that weaned a kid, and 0.02 ± 0.02 for 27 females that did not; Table 1). Kid survival to 1 year was also independent of maternal rank (residuals of social rank averaged 0.005 for both groups of females; Table 1). Adding age² to the analyses did not modify the final models.

Because we weighed very few adult females in 1994–1997, we could not include mass in the logistic regression models. We weighed several females, however, during the summers of 1990–1993 and with these values added to the captures of 1994–1997, we analysed the effects of female body mass on kid survival. To control for seasonal weight gain, we adjusted female mass to 15 July using the average summer mass gain rate for adult females (Côté et al. 1998). Females whose kid survived to weaning were on average 7.8 kg heavier than females whose kid died during the summer (t test: $t_{40} = -3.23$, $P=0.002$; Fig. 3). Similarly, females whose kid survived to one year were 6.5 kg heavier in mid-summer than females whose kid died ($t_{35} = -3.04$, $P=0.005$; Fig. 3). Body mass increased with age among adult females (curvilinear regression: $F_{2,77}=59.6$, $P<0.0001$, $R^2=0.61$; Fig. 4), but conducting the analyses with the residuals of adjusted body mass on age did not change the relationships between maternal mass and kid survival (weaning: $t_{40} = -3.6$, $P=0.0009$; 1 year old: $t_{35} = -2.8$, $P=0.007$). Furthermore, maternal age did not affect kid survival to weaning, or to 1 year, in the logistic regression models. Females that were heavy for their age, therefore, had higher reproductive success than females that were light for their age. Social rank did not affect these relationships, because neither social rank nor age-specific social rank was correlated with adult female mass (Côté 2000b).

Adult Female Survival

Once age was accounted for, adult female overwinter survival was not related to the previous summer's social rank. The residuals of social rank on age of females that survived (0.001 ± 0.008 , $N=155$) or died overwinter (-0.006 ± 0.031 , $N=13$) were similar (t test: $t_{166} = -0.23$, $P=0.8$) for all years pooled.

DISCUSSION

Kid Production

Because life history theory predicts that reproductive effort should increase with age (Stearns 1992), we expected female reproductive success to improve with age. Kid production increased with maternal age up to 9 years. The decrease in kid production among females over 9 years old, most of which were high-ranking, was probably due to reproductive senescence (Clutton-Brock 1984;

Table 1. Multiple logistic regression model showing the effects of age and social rank on the reproductive success of female mountain goats at Caw Ridge (Alberta), 1994–1997

	$\beta \pm SE$	<i>R</i>	<i>P</i>
Kid production (N=156)			
Variables in the equation:			
Residuals of rank*	33.4±9.1	0.23	0.0002
Age	2.0±0.4	0.31	<0.0001
Age ²	-0.11±0.03	-0.28	<0.0001
Residuals of rank*age	-3.7±1.0	-0.24	0.0002
Constant	-7.2±1.6		<0.0001
Kid survival to autumn (4 months) (N=95)			
Variables in the equation:			
Constant	0.9±0.2		0.0001
Variables not in the equation:			
Residuals of rank		0	0.4
Age		0	0.3
Kid survival to 1 year (N=92)			
Variables in the equation:			
Constant	0.09±0.2		0.7
Variables not in the equation:			
Residuals of rank		0	1.0
Age		0	0.4

*Because age and social rank were strongly positively correlated (Côté 2000b), we used the residuals of social ranks on age in the analyses.

Bérubé et al. 1999). Some old females continued to reproduce until they died, suggesting that reproductive senescence occurred only in a subset of females surviving to old age (see also Côté & Festa-Bianchet 2001a). Although female goats require several years to reach asymptotic mass (Fig. 4), our results suggest that reproductive senescence may occur earlier than in bighorn sheep, an ungulate of similar size, where it starts at about 13 years of age (Bérubé et al. 1999). Bailey (1991) also found that female mountain goats 10 or more years old had lower reproductive success, although in his study the difference between prime-aged (4–9 years old) and old females was not significant.

Females that were dominant for their age had a higher probability of producing a kid than females that were subordinates. In red deer, *Cervus elaphus*, hind social rank is positively correlated with lifetime reproductive success (Clutton-Brock et al. 1984, 1986). Similarly, maternal social rank is positively related to the number of lambs produced by female Barbary sheep, *Ammotragus lervia* (Cassinello & Alados 1996). Age-specific social rank appears to be an important determinant of reproductive success in female mountain goats, especially among young females. Selighsohn (1987) obtained similar results in feral ponies, *Equus caballus*: reproductive success

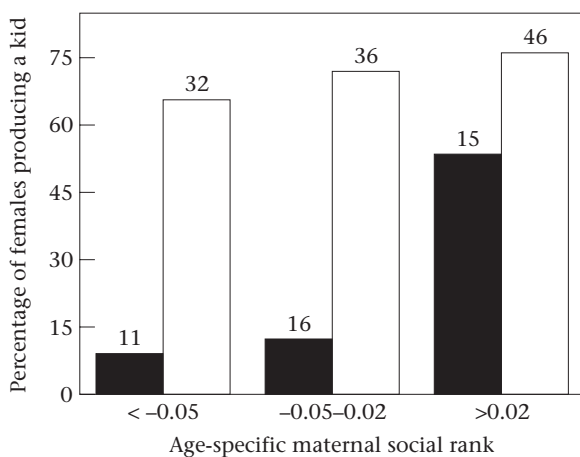


Figure 2. Kid production in relation to age-specific maternal social rank in mountain goats on Caw Ridge, Alberta, 1994–1997. ■: 3–5-year-old females; □: ≥6-year-old females. We used the residuals of social rank on age because the two variables were strongly correlated.

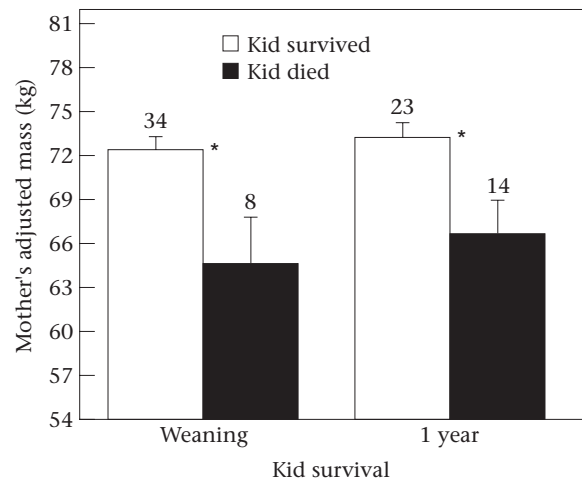


Figure 3. Maternal mass (adjusted to 15 July) of surviving and nonsurviving mountain goat kids at Caw Ridge, Alberta, 1990–1997. Sample sizes and SE are shown above each histogram. Asterisks indicate a significant difference ($P < 0.01$) in mother's adjusted mass for kids that survived or not to weaning or to 1 year.

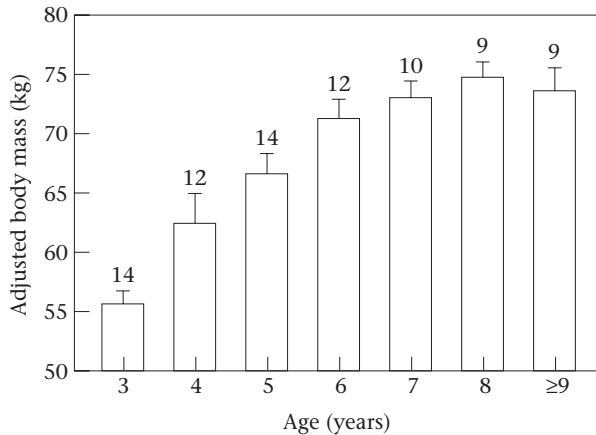


Figure 4. Body mass of adult female mountain goats as a function of age at Caw Ridge, Alberta, 1988–1997. Mass was adjusted to 15 July. Sample sizes and SE are shown above each histogram.

increased with a mare's social rank but the effect was particularly important among young females. It appears therefore that the advantages gained with dominance play a predominant role during the first part of a female's reproductive life, but have little influence on fecundity at old ages. However, it is unknown whether increased kid production by young high-ranking females entails reproductive costs later in life. Because social rank is highly stable between years in goats (Côté 2000b), advantages in terms of kid production associated with high rank have the potential to increase substantially the lifetime reproductive success of females. Even if it led to a slight reproductive cost at a later age, an association between dominance and early reproductive success is likely to be advantageous because female goats aged 3–7 years face a yearly risk of dying of about 10% (Gaillard et al. 1998) and therefore an increase in early reproduction is likely to confer a selective advantage (Stearns 1992).

Dominant female goats appear to be of better quality than subordinate females because social rank was negatively related to fluctuating asymmetry in horn characteristics (Côté & Festa-Bianchet, *in press*). Low fluctuating asymmetry may indicate high phenotypic quality because high-quality individuals should be better able to control their development and therefore should have relatively low levels of asymmetry (Gangestad & Thornhill 1999). Females with symmetrical horns had higher long-term reproductive success and greater age-specific mass than asymmetrical females (Côté & Festa-Bianchet 2001a). We weighed only 24 adult females during the period when we studied dominance relationships (1994–1997). High-ranking females were not heavier than low-ranking females when age was accounted for (Côté 2000b). Similarly, mass is not related to social rank in other ungulates (Rutberg 1983; Thouless & Guinness 1986). We are confident, therefore, that our measure of social rank was not affected by mass.

For many social mammals (dwarf mongoose, *Helogale parvula*: Rood 1980; gelada baboon, *Theropithecus gelada*: Dunbar 1980; naked mole-rat, *Heterocephalus glaber*: Jarvis 1981; prairie vole, *Microtus ochrogaster*: Carter et al. 1986),

it has been suggested that subordinate females have a lower reproductive success than dominant females because subordinates suffer more social stress (see also Harcourt 1987). This is because they are more often the target of interactions and are more susceptible to miscarriage or delayed conception (Dunbar 1980). Although physiological evidence is not available, we believe that social stress in mountain goats is unlikely to explain the lower reproductive success of subordinate females, because dominant females interacted more often with other dominant females than with females that were distant in the hierarchy (Côté 2000b). Rutberg (1986) obtained similar results for bison, *Bison bison*.

As reported by Festa-Bianchet et al. (1994), we found that most female mountain goats at Caw Ridge produced their first kid at 4–5 years old, 2–3 years later than other ungulates of similar body size (Ozoga & Verme 1986; Festa-Bianchet et al. 1995; Byers 1997; San José et al. 1999). In addition, primiparity was later at Caw Ridge than in introduced populations of mountain goats (Houston & Stevens 1988; Bailey 1991). These results suggest that females in our study population grow slowly (see also Fig. 4), and that the costs of reproducing at a young age are probably high (see also Lunn et al. 1994). High-ranking females first reproduce at a younger age than low-ranking females in red deer (Clutton-Brock et al. 1984) and in captive Cuvier's gazelle, *Gazella cuvieri*, but not in Dama gazelles, *Gazella dama* (Alados & Escós 1992). Contrary to our prediction, social rank did not affect the age of primiparity in mountain goats perhaps because of the low population density. At a higher density, social rank might affect age of primiparity, but at this stage we have no evidence of density dependence in any vital rate at Caw Ridge (Côté & Festa-Bianchet 2001b). Alternatively, if costs of reproducing at a young age are high, young high-ranking females may delay reproducing in order not to affect their long-term survival. Life span is a very important determinant of lifetime reproductive success in female ungulates (Clutton-Brock 1988). Further research on the costs of early primiparity under different environmental conditions is likely to provide a better understanding of the factors determining the timing of first reproduction (Festa-Bianchet et al. 1995).

Survival

Offspring survival is one of the most important sources of variation in lifetime reproductive success in mammals (Clutton-Brock 1988; Wasser & Norton 1993). A higher mortality for offspring of low-ranking than high-ranking females, especially for sons, has been found in several mammals (Clutton-Brock et al. 1986; Lloyd & Rasa 1989; Wasser & Norton 1993; Packer et al. 1995; Pusey et al. 1997). Contrary to our prediction, however, maternal age and social rank did not affect kid survival in mountain goats, indicating that an increase in maternal experience or dominance status does not necessarily lead to greater weaning success. In addition, maternal age and social rank were not related to kid body mass (Côté & Festa-Bianchet 2001b), suggesting that maternal expenditure does not vary according to age or rank in mountain

goats (but see Côté & Festa-Bianchet 2001a). Other researchers have also found that maternal age does not affect offspring survival in ungulates, particularly when primiparous or very old individuals are excluded (bighorn sheep: Bérubé et al. 1999; captive Barbary sheep: Cassinello & Alados 1996; horses: Monard et al. 1987; moose, *Alces alces*: Keech et al. 2000; roe deer, *Capreolus capreolus*: Andersen & Linnell 1998). In other species, however, mature mothers are more successful at rearing offspring than young mothers, until the onset of reproductive senescence (pronghorn, *Antilocapra americana*: Byers 1997; red deer: Clutton-Brock 1984; white-tailed deer, *Odocoileus virginianus*: Ozoga & Verme 1986).

Although the majority of our females reproduced before reaching full adult mass, we have shown that kids born to females that were heavy for their age survived better to weaning and to 1 year than the kids of light females. Similarly, roe deer fawns have a lower risk of dying during summer if they are born to heavy does (Andersen & Linnell 1998). A higher body mass is likely to be associated with a higher capacity for maternal care, especially in a capital breeder, where individuals may rely on stored resources to sustain the costs of reproduction, such as the mountain goat (Jönsson 1997). Our data suggest that large females provided more maternal care, as kid mass during summer was correlated with maternal mass (Côté & Festa-Bianchet 2001b; see also Andersen et al. 2000 for an example in an income breeder who use the energy acquired during the reproductive period to offset reproductive costs). In contrast, Festa-Bianchet & Jorgenson (1998) found a very weak relationship between maternal and lamb mass in bighorn sheep. Festa-Bianchet et al. (1998), however, found that in bighorn lambs survival to weaning increases with maternal mass. In addition, individual ewes were lighter in a year before their lamb died than in a year before their lamb survived to weaning (Festa-Bianchet 1998).

Because high social rank gives priority of access to food in several ungulates (Rutberg 1986; Masteller & Bailey 1988; Thouless 1990) dominance may confer a survival advantage in adults. Few studies, however, have examined the relationship between dominance and adult survival in large mammals. Overwinter survival in adult female red deer (Gomendio et al. 1990) and pronghorn (Byers 1997) is not related to dominance rank. Similarly, social dominance did not affect overwinter survival in female mountain goats but, as in pronghorn (Byers 1997), social rank was not related to foraging efficiency in summer (Fournier & Festa-Bianchet 1995).

In conclusion, the reproductive success of female mountain goats is affected by both age and social dominance. Kid production increased with maternal social rank, independently of age. The mechanism leading to greater kid production with increasing social rank is unknown. More high-ranking females may reach the condition threshold to enter oestrus than low-ranking females or, alternatively, they may have fewer miscarriages. To understand fully the reproductive strategies of females, further research should assess whether maternal expenditure and costs of reproduction vary according to maternal rank, age and offspring sex.

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References

- Alados, C. L. & Escós, J. M. 1992. The determinants of social status and the effect of female rank on reproductive success in Dama and Cuvier's gazelles. *Ethology, Ecology and Evolution*, **4**, 151–164.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.
- Andersen, R. & Linnell, J. D. C. 1998. Ecological correlates of mortality of roe deer fawns in a predator-free environment. *Canadian Journal of Zoology*, **76**, 1217–1225.
- Andersen, R., Gaillard, J.-M., Linnell, J. D. C. & Duncan, P. 2000. Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology*, **69**, 672–682.
- Arnabom, T., Fedak, M. A. & Rothery, P. 1994. Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. *Behavioral Ecology and Sociobiology*, **35**, 373–378.
- Bailey, J. A. 1991. Reproductive success in female mountain goats. *Canadian Journal of Zoology*, **69**, 2956–2961.
- Berger, J. 1986. *Wild Horses of the Great Basin, Social Competition and Population Size*. Chicago: Chicago University Press.
- Bérubé, C. H., Festa-Bianchet, M. & Jorgenson, J. T. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, **80**, 2555–2565.
- Brandborg, S. M. 1955. Life history and management of the mountain goat in Idaho. *Idaho Wildlife Bulletin*, **2**, 1–142.
- Byers, J. A. 1997. *American Pronghorn: Social Adaptations and the Ghosts of Predators Past*. Chicago: University of Chicago Press.
- Cameron, E. Z., Linklater, W. L., Stafford, K. J. & Minot, E. O. 2000. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behavioral Ecology and Sociobiology*, **47**, 243–249.
- Carter, C. S., Getz, L. L. & Cohen-Parsons, M. 1986. Relationships between social organisation and behavioural endocrinology in a monogamous mammal. *Advance Studies of Behavior*, **16**, 109–145.
- Cassinello, J. & Alados, C. L. 1996. Female reproductive success in captive *Ammotragus lervia* (Bovidae, Artiodactyla). Study of its components and effects of hierarchy and inbreeding. *Journal of Zoology*, **239**, 141–153.

- Clover, M. R. 1956. Single-gate deer trap. *California Fish and Game*, **42**, 199–201.
- Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Clutton-Brock, T. H. (Ed.) 1988. *Reproductive Success*. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*, **308**, 358–360.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131–133.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour*, **34**, 460–471.
- Côté, S. D. 1999. Dominance sociale et traits d'histoire de vie chez les femelles de la chèvre de montagne (in English). Ph.D. thesis, Université de Sherbrooke.
- Côté, S. D. 2000a. Determining social rank in ungulates: a comparison of aggressive interactions recorded at a bait site and under natural conditions. *Ethology*, **106**, 945–955.
- Côté, S. D. 2000b. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour*, **137**, 1541–1566.
- Côté, S. D. & Beaudoin, C. 1997. Grizzly bear (*Ursus arctos*) attacks and nanny-kid separation on mountain goats (*Oreamnos americanus*). *Mammalia*, **61**, 614–617.
- Côté, S. D. & Festa-Bianchet, M. 2001a. Offspring sex ratio in relation to maternal age and social rank in mountain goats *Oreamnos americanus*. *Behavioral Ecology and Sociobiology*, **49**, 260–265.
- Côté, S. D. & Festa-Bianchet, M. 2001b. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia*, **127**, 230–238.
- Côté, S. D. & Festa-Bianchet, M. In press. Life-history correlates of horn asymmetry in mountain goats. *Journal of Mammalogy*.
- Côté, S. D., Festa-Bianchet, M. & Fournier, F. 1998. Life-history effects of chemical immobilization and radiocollars on mountain goats. *Journal of Wildlife Management*, **62**, 745–752.
- Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour*, **125**, 283–313.
- Dunbar, R. I. M. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioral Ecology and Sociobiology*, **7**, 253–265.
- Dunbar, R. I. M. & Dunbar, P. 1977. Dominance and reproductive success among female gelada baboons. *Nature*, **266**, 351–352.
- Ellis, L. 1995. Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Sociobiology*, **16**, 257–333.
- Festa-Bianchet, M. 1988. Age-specific reproduction of bighorn ewes in Alberta, Canada. *Journal of Mammalogy*, **69**, 157–160.
- Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. *Animal Behaviour*, **42**, 71–82.
- Festa-Bianchet, M. 1998. Condition-dependent reproductive success in bighorn ewes. *Ecology Letters*, **1**, 91–94.
- Festa-Bianchet, M. & Jorgenson, J. T. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology*, **9**, 144–150.
- Festa-Bianchet, M., Urquhart, M. & Smith, K. G. 1994. Mountain goat recruitment: kid production and survival to breeding age. *Canadian Journal of Zoology*, **72**, 22–27.
- Festa-Bianchet, M., Jorgenson, J. T., Lucherini, M. & Wishart, W. D. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology*, **76**, 871–881.
- Festa-Bianchet, M., Gaillard, J. M. & Jorgenson, J. T. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, **152**, 367–379.
- Fournier, F. & Festa-Bianchet, M. 1995. Social dominance in adult female mountain goats. *Animal Behaviour*, **49**, 1449–1459.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.
- Gangestad, S. W. & Thornhill, R. 1999. Individual differences in developmental precision and fluctuating asymmetry: a model and its implications. *Journal of Evolutionary Biology*, **12**, 402–416.
- Geist, V. 1967. On fighting injuries and dermal shields of mountain goats. *Journal of Wildlife Management*, **31**, 192–194.
- Gomendio, M., Clutton-Brock, T. H., Albon, S. D., Guinness, F. E. & Simpson, M. J. 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature*, **343**, 261–263.
- Hand, J. L. 1986. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. *Quarterly Review of Biology*, **61**, 201–220.
- Harcourt, A. H. 1987. Dominance and fertility among female primates. *Journal of Zoology*, **213**, 471–487.
- Haviernick, M., Côté, S. D. & Festa-Bianchet, M. 1998. Immobilization of mountain goats with xylazine and reversal with idazoxan. *Journal of Wildlife Diseases*, **34**, 342–347.
- Houston, D. B. & Stevens, V. 1988. Resource limitation in mountain goats: a test by experimental cropping. *Canadian Journal of Zoology*, **66**, 228–238.
- Jarvis, J. U. M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*, **212**, 571–573.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, **78**, 57–66.
- Jorgenson, J. T., Samson, J. & Festa-Bianchet, M. 1990. Immobilization of bighorn sheep with xylazine hydrochloride and reversal with idazoxan. *Journal of Wildlife Diseases*, **26**, 522–527.
- Keech, M. A., Bowyer, R. T., Ver Hoef, J. M., Boertje, R. D., Dale, B. W. & Stephenson, T. R. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management*, **64**, 450–462.
- LeBoeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist*, **14**, 163–176.
- Livezey, K. B. 1990. Toward the reduction of marking-induced abandonment of newborn ungulates. *Wildlife Society Bulletin*, **18**, 193–203.
- Lloyd, P. H. & Rasa, O. A. E. 1989. Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behavioral Ecology and Sociobiology*, **25**, 411–420.
- Locati, M. & Lovari, S. 1991. Clues for dominance in female chamois: age, weight, or horn size. *Aggressive Behavior*, **17**, 11–15.
- Lunn, N. J., Boyd, I. L. & Croxall, J. P. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, **63**, 827–840.
- McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models*. London: Chapman & Hall.
- Masteller, M. A. & Bailey, J. A. 1988. Agonistic behavior among mountain goats foraging in winter. *Canadian Journal of Zoology*, **66**, 2585–2588.
- Monard, A. M., Duncan, P., Fritz, H. & Feh, C. 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behavioral Ecology and Sociobiology*, **41**, 243–249.
- Noldus Information Technology 1998. *Matman, Reference Manual, Version 1.0 for Windows*. Wageningen: Noldus Information Technology.

- van Noordwijk, M. A. & van Schaik, C. P. 1987. Competition among female long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, **35**, 577–589.
- Ozoga, J. J. & Verme, L. J. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. *Journal of Wildlife Management*, **50**, 480–486.
- Packer, C., Collins, D. A., Sindimwo, A. & Goodall, J. 1995. Reproductive constraints on aggressive competition in female baboons. *Nature*, **373**, 60–63.
- Pusey, A., Williams, J. & Goodall, J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, **277**, 828–831.
- Reiter, J., Panken, K. J. & LeBoeuf, B. J. 1981. Female competition and reproductive success in northern elephant seals. *Animal Behaviour*, **29**, 670–687.
- Rood, J. P. 1980. Mating relationships and breeding suppression in the dwarf mongoose. *Animal Behaviour*, **28**, 143–150.
- Rutberg, A. T. 1983. Factors influencing dominance status in American bison cows (*Bison bison*). *Zeitschrift für Tierpsychologie*, **63**, 206–212.
- Rutberg, A. T. 1986. Dominance and its fitness consequences in American bison cows. *Behaviour*, **96**, 62–91.
- Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia*, **106**, 212–220.
- San José, C., Braza, F. & Aragón, S. 1999. The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*). *Canadian Journal of Zoology*, **77**, 1717–1722.
- Schall, R. 1991. Estimation in generalized linear models with random effects. *Biometrika*, **78**, 719–727.
- Selighsohn, E. V. 1987. Dominance relationships and reproductive success within bands of feral ponies. Ph.D. thesis, University of Connecticut.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stevens, V. & Houston, D. B. 1989. Reliability of age determination of mountain goats. *Wildlife Society Bulletin*, **17**, 72–74.
- Thouless, C. R. 1990. Feeding competition between grazing red deer hinds. *Animal Behaviour*, **40**, 105–111.
- Thouless, C. R. & Guinness, F. E. 1986. Conflict between red deer hinds: the winner always wins. *Animal Behaviour*, **34**, 1166–1171.
- de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, **50**, 1375–1389.
- de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, **55**, 827–843.
- Wasser, S. K. & Norton, G. 1993. Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behavioral Ecology and Sociobiology*, **32**, 273–281.
- Wauters, L. A., de Crombrughe, S. A., Nour, N. & Matthysen, E. 1995. Do female roe deer in good condition produce more sons than daughters. *Behavioral Ecology and Sociobiology*, **37**, 189–193.
- Wolff, J. O. 1998. Breeding strategies, mate choice, and reproductive success in American bison. *Oikos*, **83**, 529–544.