

Yanick Gendreau · Steeve D. Côté ·
Marco Festa-Bianchet

Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*)

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Abstract Little is known about maternal effects on post-weaning development, yet they may be important because maternal care could have long-term consequences only evident when offspring approach adulthood. We have assessed the effects of maternal age, current reproduction (presence of a kid of the year) and social rank on the body mass, horn length and social rank of 1- and 2-year-old mountain goats (*Oreamnos americanus*). Maternal reproductive status and social rank did not affect the mass or horn length of either yearlings or 2-year-olds. Maternal age was positively correlated with yearling body mass for males but not females. We could not detect any maternal age effects on body mass of 2-year-olds. Maternal age and spring forage quality were positively correlated with horn length of yearlings of both sexes, but not of 2-year-olds. Juvenile females showed compensatory growth in mass between 1 and 2 years of age, but males did not. Neither sex showed compensatory growth in horn length. None of the maternal characteristics we examined directly affected the social rank of juveniles, which increased with body mass. Social rank in female mountain goats seems to be established early in life and maintained to adulthood. By affecting yearling development, maternal age could affect the reproductive success of males.

Keywords Post-weaning care · Maternal investment · Reproduction · Social rank · Horn growth

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Y. Gendreau · M. Festa-Bianchet
Département de Biologie, Université de Sherbrooke,
Sherbrooke, QC, J1K 2R1, Canada

S. D. Côté (✉)
Département de Biologie and Centre d'études nordiques,
Université Laval,
Québec, QC, G1K 7P4, Canada
e-mail: steeve.cote@bio.ulaval.ca
Tel.: +1-418-6562131, #3490
Fax: +1-418-6562043

Introduction

The expression of several fitness-related traits can be affected by genotype, environment and parental care (Cheverud 1984). Parents may affect the expression of offspring phenotype by contributing to their genotype and by providing care (Kirkpatrick and Lande 1989). Although the effects of maternal characteristics such as age or body condition on offspring phenotype during the nursing period have been widely studied in mammals (Boness and Bowen 1996; Andersen et al. 2000; Bales et al. 2002; Weladji et al. 2003), few studies have examined maternal effects after weaning (Bernardo 1996). Post-weaning maternal effects may be important because maternal care could have long-term consequences that may not be evident until offspring approach adulthood (Clutton-Brock 1991).

Maternal age could affect the post-weaning development of offspring. The terminal investment theory (Clutton-Brock 1984; Stearns 1992) predicts that as mothers age they should increase maternal investment because their reduced survival probability decreases their future reproductive potential. Old females, however, may be affected by reproductive senescence and be unable to provide much maternal care (Bérubé et al. 1999; Kirkwood and Austad 2000). In species with protracted maternal care, mothers nursing a young of the year may face a three-way trade-off in allocating care between a physiologically weaned but behaviourally dependent juvenile, a current nursing offspring, and future offspring. Maternal care is essential for survival of the young of the year, but because physiologically weaned juveniles have a higher chance of survival than young of the year (Gaillard et al. 2000), mothers may obtain greater fitness returns by allocating care to juveniles.

Another maternal characteristic that may affect post-weaning development is social rank. Several studies have shown a positive effect of maternal rank on the early development of offspring (Clutton-Brock et al. 1986;

Kojola 1997; von Holst et al. 2002). Higher social rank may allow dominant females better access to food at critical times (Barrette and Vandal 1986). The offspring of dominant mothers may then enjoy better access to high-quality food (Barrette and Vandal 1986; Cassinello 2002), a reduction of time spent in alert behaviour, and more time available for foraging (Berger 1978) compared to independent offspring or to offspring associated with subordinate mothers.

We assessed the effects of maternal age, reproductive status and social rank on body mass, horn length, and social development of juvenile mountain goats aged 1 or 2 years. Because food abundance and quality may play an important role in early development (Verme 1989), our analyses also accounted for variability in spring forage quality. About 60% of yearling goats and a few 2-year-olds are behaviourally associated with their mother (S.D. Côté, unpublished data). Some females, therefore, may continue to provide maternal care after physiological weaning, which occurs at about 5–7 months of age (S.D. Côté, unpublished data). Juveniles that remain with their mother may enjoy more maternal care and grow faster than those (about 40%) that become independent (Brookshier and Fairbanks 2003). Because of the long juvenile period (from physiological weaning to first reproduction at 3 to 5 years of age; Côté and Festa-Bianchet 2003), there may be long-lasting effects of maternal characteristics on juveniles. Consequently, this long-term study of a large mammal with variable duration of maternal care afforded a unique opportunity to assess the effects of maternal characteristics on the development and social rank of weaned juveniles.

Methods

We studied mountain goats on Caw Ridge, west-central Alberta, Canada (54°N, 119°W), a mountain complex east of the front range of the Rocky Mountains. Mountain goats use 28 km² of alpine tundra and subalpine forest at elevations of 1,750–2,185 m. The population, studied intensively since 1989, has ranged from 76 to 147 individuals, including between 35 and 59 females aged 2 years or older. Here we use data collected from 1990 to 2002.

Adult mountain goats are sexually segregated and dimorphic: in mid-summer, males aged 5 years and older weigh about 102 kg and females 71 kg (Côté and Festa-Bianchet 2003). Adult females live in nursery groups with kids, yearlings and 2-year-olds. Kids of both sexes weigh approximately 13–14 kg in mid-summer and sexual dimorphism develops post-weaning, over several years. Yearling males are about 10% heavier than yearling females and 2-year-old males are about 15% heavier than 2-year-old females (Côté and Festa-Bianchet 2003). In our study population, most females are primiparous at 4 or 5 years of age (Côté and Festa-Bianchet 2001a) and a single kid is produced in almost all cases. There have been no cases of twinning since 1991. Over 80% of kids are born within a 2-week period in late May and early June,

and on average 60.3% of kids survive to 1 year (Côté and Festa-Bianchet 2001b). We have not documented any cases of immigration or emigration for yearlings at Caw Ridge (Côté and Festa-Bianchet 2003), therefore we assume that all kids that survived the winter are observed as yearlings.

We captured 288 goats in remotely controlled box traps and self-tripping nylon mesh Clover traps baited with salt, mostly from early June to mid-September. We used a long pole syringe to immobilise goats 2 years and older with an intramuscular injection of xylazine hydrochloride, whose effects were later reversed with idazoxan (Côté et al. 1998a; Haviernick et al. 1998). Large yearlings were also drugged before handling. We marked animals with visual collars, Allflex plastic ear tags or radio-collars. After 1997, we did not capture kids or lactating females because of the risk of kid abandonment (Côté et al. 1998a). All adult females (≥ 3 years) were marked during this study.

Most goats (92%) were marked before they were 3-year-olds. We aged goats that were adults at their first capture by the number of horn annuli, a technique reliable up to about age 7 (Stevens and Houston 1989). We measured horn length and base circumference to the nearest millimetre, and weighed captured goats with a spring scale to the nearest 0.5 kg (Côté et al. 1998a). In 2001 and 2002, we used two electronic platform scales to weigh 45 and 73 marked individuals without handling them. Available data on mother's body mass, however, were insufficient to include this variable in the analyses.

Goats were observed almost daily from mid-May to mid-September, with spotting scopes ($\times 15$ – 45) at distances of 200–700 m. We determined maternal reproductive status (lactating or not) by the repeated observations of a marked mother with a kid during the summer. Mothers whose kid died before 15 July were considered as not lactating. Kid sex was determined by urination posture and observation of a vulvar patch (Côté and Festa-Bianchet 2003).

Following Gaillard et al. (2000), we considered the juvenile period as the time from physiological weaning to the minimum age of first reproduction. In mountain goats, weaning occurs during the first autumn/winter and the earliest primiparity is at 3 years of age (Côté and Festa-Bianchet 2001a). Therefore, we only considered juvenile goats aged 1 and 2 years in our analyses. The age of first reproduction for males is unknown, but they are unlikely to breed before 3 years of age (Geist 1964).

At Caw Ridge, 52% of males ($N = 62$) and 68% of females ($N = 82$) associated with their mother as yearlings, and 8% ($N = 111$ both sexes combined) as 2-year-olds. A juvenile was considered to be associated with its mother when it was observed feeding or resting within 1 m of her on >30 days during summer. All 18 associated yearlings that were marked as kids associated only with their mother. Juveniles were not considered associated if the association ended before 15 July.

To estimate yearly variability in vegetation quality we used fecal crude protein (FCP; Côté and Festa-Bianchet 2001b; Blanchard et al. 2003). Fecal pellets were dried and analysed with the macro-Kjeldhal acid digestion technique

Table 1 Characteristics of the annual social hierarchies in yearling and 2-year-old mountain goats of both sexes at Caw Ridge, Alberta. *h* is the Landau's (1951) linearity index and *h'* is the linearity index corrected for unknown relationships (de Vries 1995). Inconsistencies are cases where lower-ranked individuals dominate higher-ranked ones

Year	Age	<i>h</i>	<i>h'</i> (linearity)	<i>P</i> -values ^a	Number of inconsistencies	% of dyads observed	Number of interactions observed	Ratio of individuals included in the analysis ^b
1994	2	0.30	0.46	0.37	0	52	21	7/8
1995	2	0.30	0.39	0.03	1	49.5	105	15/18
1996	2	0.16	0.33	0.44	0	36	36	9/10
1998	2	0.23	0.42	0.41	0	43	21	7/8
2001	2	0.17	0.27	0.25	0	43	91	14/14
2002	2	0.41	0.46	0.0008	5	65	136	17/17
2001	1	0.20	0.28	0.06	4	43	153	18/19

^a Based on 10,000 randomisations implemented in Matman 1.0, see Methods. The *P* values refer to the test of linearity

^b Individuals included in the calculation of social rank/total number of individuals of the same age present in the same year. See text for details

(Association of Official Analytical Chemist 1980). We used FCP in early June, which is correlated with kid mass in midsummer, as an index of the timing of the initiation of vegetation growth (Côté and Festa-Bianchet 2001b). Fecal crude protein is a reliable indicator of forage quality (O'Donovan et al. 1963; Festa-Bianchet 1988) and has often been used in the study of wild ungulates (Festa-Bianchet 1988; Côté and Festa-Bianchet 2001b). Annual variations in FCP are likely to be due to difference in weather, particularly temperature and the duration of snow cover. We determined FCP just after the peak parturition period (1 June \pm 2 days), because late spring appears to be a crucial period for the nutrition of lactating females (Portier et al. 1998). To examine the possibility of multi-year effects, we compared juvenile mass to crude protein values both in the year of birth and in the current year.

From 1994 to 1998 and in 2001–2002, we recorded agonistic interactions between adult females and between juveniles using all-occurrences sampling and focal observations (Altmann 1974). We constructed separate dominance hierarchies each year for yearlings, 2-year-olds and adult females. For each age class we only constructed hierarchies during years when more than 80% of individuals were seen to interact with at least 20% of all possible opponents. Juveniles of both sexes were pooled in a single matrix to assess rank. We considered yearlings and 2-year-olds separately because of the strong effect of age on social rank (Côté 2000) and because yearlings averaged only 69% of the mass of 2-year-olds (Côté and Festa-Bianchet 2003). We observed enough interactions to construct social hierarchies in the years 1994–1997 (Côté 2000), 2001 and 2002 for adult females, 1994–1996, 1998, 2001 and 2002 for 2-year-olds, and only 2001 for yearlings. To order individuals in a hierarchy, we followed de Vries (1998), using Matman 1.0 for Windows (Noldus Information Technology 1998). We calculated the linearity of annual dominance hierarchies with the index *h'* (de Vries 1995; Côté 2000), which varies from 0 (no linearity) to 1 (perfect linearity). To determine if *h'* was statistically significant, a sampling process using 10,000 randomi-

sations was performed to compare matrices (de Vries 1995). Then, the dominance hierarchy was reorganised by an iterative procedure to minimise inconsistencies (de Vries 1995, 1998; Côté 2000). Inconsistencies arise when individual A dominates B, but A is ranked below B in the hierarchy (de Vries 1998). Each year, hierarchies for adult females were strongly linear (Côté 2000). Although yearly hierarchies were not always significantly linear for yearlings and 2-year-olds (Table 1), we used the rank order after minimising inconsistencies, because most hierarchies included no inconsistencies (Table 1). Non-significant linearities were likely due to a large proportion of unknown relationships in the matrix (Galimberti et al. 2003). The low number of inconsistencies reflects high transitivity of rank and suggests a hierarchical social organisation among juveniles. Because the number of individuals varied between years, to compare rank values obtained in different years we standardised social rank by $1 - (\text{rank}/\text{NI})$, where NI is the number of individuals in an age class during year I (Côté 2000). Therefore, social rank varied between 0 (subordinate) and 1 (dominant). Because social rank is highly related to age for adult females, we used the residuals of the regression between age and social rank in analyses for this group (Côté 2000; Côté and Festa-Bianchet 2001a).

To determine whether aggressive behaviour from adult females towards juveniles depended on maternal characteristics, we conducted 30-min focal observations on yearlings and 2-year-olds. We noted all aggressive interactions between the focal animal and all adult females other than the mother occurring during each focal sample. Because opportunities for social encounters varied between samples, we divided the number of interactions initiated by adult females on the juvenile by the total number of opportunities (Côté 2000). Opportunities were defined as situations where an adult female other than the mother initiated an approach within 4 m of the focal juvenile (Côté 2000). Focals during which no opportunity of interaction occurred were excluded. We used the average value of aggressiveness when >1 focal for the same individual was available, and only analysed samples during which the focal juvenile was active >20 min.

Statistical analyses

To adjust body mass and horn length to 15 July we used the slopes of linear regressions of body mass and horn length measurements on capture date (Côté et al. 1998a). Separate regressions were performed for yearlings and 2-year-olds of each sex. We used the average of both horns to measure horn length. We monitored 55 yearlings and 36 two-year-olds with known mothers. To account for stochastic year effects (the 55 yearlings were born over 11 years and the 36 two-year-olds were born over 12 years), we used general linear mixed models (or GLMM) in S-Plus 2000 with year as a random term. This method reduces the chance of type 1 error by avoiding pooling data (Jenkins 2002). There were 31 mothers of yearlings and 28 mothers of 2-year-olds. Our sample sizes were insufficient for a GLMM with mother as a random term. As a general rule, mixed models can only be used when 3 times more data than groups are available (B. Steele, personal communication). When the confidence interval (95%) of a random term includes zero, there is no need to use GLMM and we used a general linear model (GLM; Pinheiro and Bates 2000). Variables were included in models if they had a P -value <0.05 using the restricted maximum likelihood (REML) procedure.

We analysed separately body mass, horn length and social rank for yearlings and 2-year-olds. Because maternal rank was not known for all mothers in all years, its inclusion reduced the sample size from 55 to 36 for yearlings and from 36 to 28 for 2-year-olds. Therefore, maternal rank was excluded from the first step of the analyses with all the independent variables and was only included in a second analysis limited to the variables retained from the

first model. If no maternal characteristics affected juvenile traits in models with and without maternal rank, we used a larger sample (including yearlings with unknown mothers) to assess the effect of juvenile sex and FCP. Because the social ranks of yearlings were only determined for 2001, we could not test the effect of maternal characteristics on yearling social development. We used a GLM to test whether yearling social rank in 2001 was affected by sex, body mass or horn length. To determine the effects of sex, body mass and horn length on the social rank of 2-year-olds, if no maternal effects were found, we included all individuals for which we had seen enough interactions to assign a rank ($N=53$). We used linear regression to test whether social rank as a yearling in 2001 was correlated with social rank at 2 years in 2002. For females, we also compared rank as a 2-year-old to rank as a 3-year-old. We tested whether maternal characteristics could affect yearling survival to age 2, either directly or indirectly through an effect on yearling body mass, using multiple logistic regressions. Finally, we assessed whether compensatory growth occurred between 1 and 2 years of age with a GLMM with year as a random term. The significance of fitted terms and of their interactions were assessed by the F values in S-Plus (Pinheiro and Bates 2000). Data are presented as means \pm SD.

Results
Body mass

In the model for yearling body mass, the confidence interval of year as a random term included zero, therefore we used a GLM (Table 2). The final model included sex,

Table 2 Generalized linear models (GLM) of the effects of maternal characteristics and spring fecal crude protein (FCP) on the body mass and horn length of yearling mountain goats at Caw Ridge Alberta, 1990–2002

Dependent variable	Variables	b \pm SE	F -value	P	df	
Yearling body mass ($N=55$)	Model		4.69	0.006	3, 51	
Total variance explained 21.6%	Sex	2.89 \pm 1.81	5.47	0.02	1	
GLM model with no random effect of year	Mother's age	0.26 \pm 0.20	3.76	0.06	1	
	Mother's age \times sex (male)	0.71 \pm 0.25	4.30	0.02	2	
	Mother's age \times sex (female)	-0.18 \pm 0.32				
	Intercept	31.77 \pm 1.81	306.7	<0.0001	1	
	Not included in the final model					
	% FCP of the current year	0.45 \pm 0.22	1.76	0.19	1	
	% FCP year of birth	-0.07 \pm 0.23	0.49	0.49	1	
	Association with mother (yes/no)	-0.73 \pm 1.02	0.55	0.46	1	
	Maternal reproductive status (kid/no kid)	-0.75 \pm 0.99	0.35	0.56	1	
		Model		12.39	<0.0001	3, 50
Yearling horn length ($N=54$)	Sex	-9.25 \pm 1.80	22.97	<0.0001	1	
Total variance explained 42.6%	% FCP of the current year	2.52 \pm 0.81	5.34	0.03	1	
GLM model with no random effect of year	Mother's age	2.36 \pm 0.79	8.86	0.005	1	
	Intercept	66.20 \pm 16.87	15.39	<0.0001	1	
	Not included in the final model					
	% FCP year of birth	1.60 \pm 0.85	3.53	0.07	1	
	Association with mother (yes/no)	2.14 \pm 1.99	1.16	0.29	1	
	Maternal reproductive status (kid/no kid)	-2.60 \pm 1.80	2.07	1.16	1	
	Mother's age \times sex	-0.71 \pm 0.73				

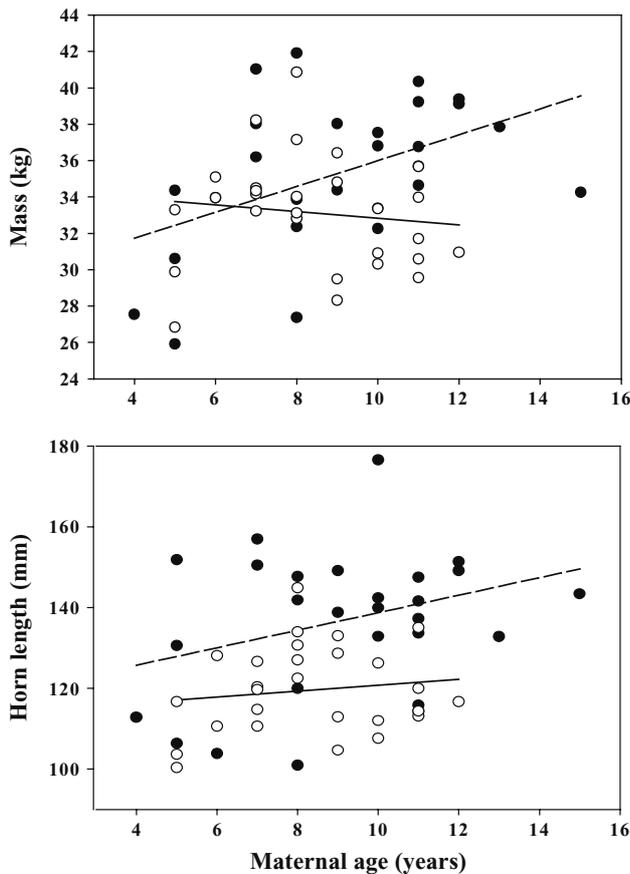


Fig. 1 Body mass and horn length of yearling male and female mountain goats born to mothers of different ages on Caw Ridge, Alberta. *Open circles and solid line = females; solid circles and dashed line = males*

maternal age and their interaction (Table 2). Yearling mass increased with maternal age for males, but not for females (Fig. 1). Adding maternal social rank to a similar model but with a smaller sample size did not explain any more variance ($F_{1,34} = 1.17, P = 0.29$).

Because females gain mass up to 6 years of age (Côté and Festa-Bianchet 2003), young mothers may face a trade-off between growth and reproduction, and higher fitness costs of reproduction compared to older mothers. Consequently, we repeated this analysis excluding mothers younger than 6 years. When young mothers were excluded, the interaction between yearling sex and maternal age was not significant ($F_{2,41} = 2.32, P = 0.11$).

The mass of 2-year-olds was only affected by sex according to a GLMM with year as a random term (variance explained by year was 7.2%; Table 3). None of the other variables had a significant effect (Table 3), including mother's age (Fig. 2). Adding maternal rank in a similar model with a smaller sample size did not increase the variance explained ($F_{1,19} = 1.17, P = 0.34$). When we compared the mass of 2-year-old males and females using all data available in a GLM, we confirmed a strong effect of sex (Côté and Festa-Bianchet 2003): males weighed on average 50.3 ± 5.0 kg and females 45.0 ± 3.9 kg ($F_{1,91} = 38.1, P < 0.0001$) with a positive effect of spring

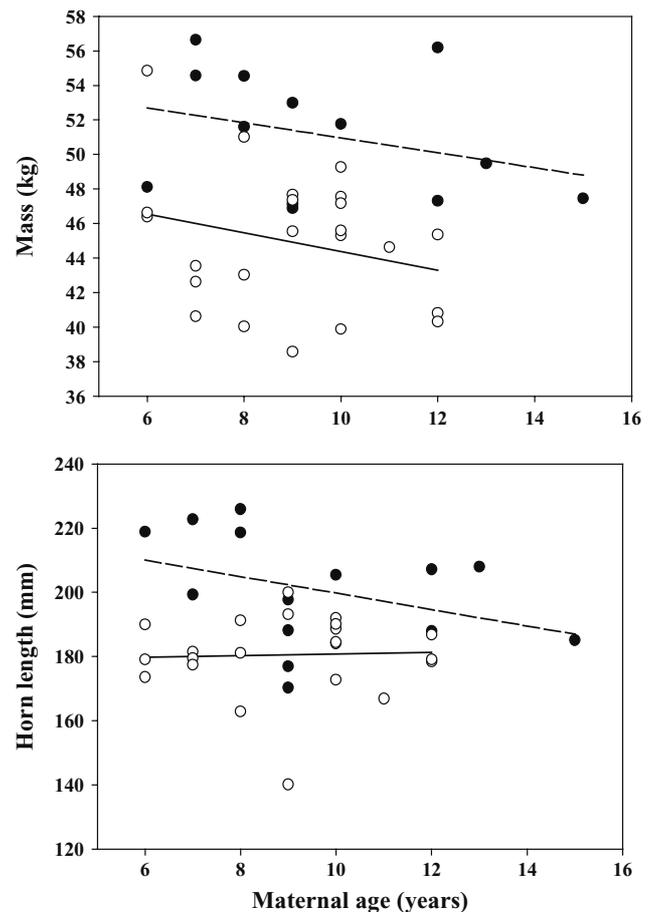


Fig. 2 Body mass and horn length of 2-year-old male and female mountain goats born to mothers of different ages on Caw Ridge, Alberta. *Open circles and solid line = females; solid circles and dashed line = males*

FCP in the current year ($F_{1,90} = 12.4, P = 0.0007$) and no effect of FCP in the year of birth ($F_{1,81} = 0.83, P = 0.11$). The final model explained 36% of the variance in mass of 2-year-olds ($F_{2,89} = 25.3, P < 0.0001$).

Horn length

The best model for yearling horn length included sex, spring crude protein of the current year and mother's age (Table 2; Fig. 1). Including maternal social rank for the sub-sample of yearlings for which this variable was available did not improve model fit ($F_{1,31} = 1.58, P = 0.12$). When mothers ≤ 6 -year-olds were excluded, maternal age no longer affected yearling horn length ($F_{1,40} = 0.05, P = 0.82$).

For 2-year-olds, only sex explained variance in horn length (Table 3; Fig. 2), and there was no effect of maternal rank ($F_{1,26} = 1.10, P = 0.3$). An analysis of the effects of sex on horn length of 2-year-olds using all available measurements, with year as a random factor (variance explained by year was 18.7% in a GLMM), confirmed the sexual dimorphism in horn length (Côté et al. 1998b): the horns of males averaged 205 ± 14 mm in length, those of females 181 ± 15 mm ($F_{1,82} = 72.3, P < 0.0001$, variance

Table 3 General linear model (GLM) and general linear mixed-model (GLMM) of the effects of maternal characteristics and spring fecal crude protein (FCP) on the body mass and horn length of 2-year-old mountain goats at Caw Ridge Alberta, 1990–2002

Dependent variables	Variables	b ± SE	F-value	P	df
Mass of 2-year-olds (N = 36)	Sex	-3.03 ± 0.67	20.57	0.0001	1, 23
Total variance explained 49.4%	Intercept	48.15 ± 0.72	4,458.0	<0.0001	1, 23
GLMM model with random effect of year (N = 12)	Not included in the final model				
	% FCP ^a of the current year	0.26 ± 0.26	1.04	0.32	1
	% FCP ^a year of birth	0.04 ± 0.23	0.03	0.86	1
	Mother's age	-0.49 ± 0.11	2.84	0.11	1
	Association with mother (yes/no)	-2.95 ± 1.70	3.02	0.10	1
	Maternal reproductive status (kid/no kid)	0.51 ± 1.50	0.12	0.74	1
	Mother's age × sex (male)	-0.45 ± 0.41	1.38	0.27	2
	Mother's age × sex (female)	-0.52 ± 0.42			
Horn length of 2-year-olds (N = 36)	Model		14.04	<0.0001	1, 34
Total variance explained 38.1%	Sex	-11.14 ± 2.44	20.92	0.0001	1
GLM model with no random effect of year	Intercept	191.5 ± 244	6182.2	<0.0001	1
	Not included in the final model				
	% FCP of the current year	-0.17 ± 1.0	0.02	0.90	1
	% FCP year of birth	-0.37 ± 1.03	0.02	0.90	1
	Mother's age	-1.27 ± 1.39	0.75	0.40	1
	Association with mother (yes/no)	0.51 ± 3.97	0.02	0.90	1
	Maternal reproductive status (kid/no kid)	0.69 ± 3.60	0.02	0.90	1
	Mother's age × sex	1.43 ± 1.25	1.29	0.27	2

^a Because % FCPs are measured annually, we tested the effect of this variable in a GLM instead of a GLMM

explained by the model 28.5%). No effects of FCP in the current year ($F_{1,93} = 2.3$, $P = 0.13$) or in the year of birth ($F_{1,85} = 2.7$, $P = 0.11$) were detected.

Social rank

The effect of sex on yearling social rank was not significant, although males appeared to have higher ranks than females ($F_{1,12} = 3.55$, $P = 0.09$). We obtained the same relationship when mass was taken into account ($F_{1,12} = 4.26$, $P = 0.06$). Because yearling mass and horn length were correlated ($r = 0.66$, $N = 112$, $P < 0.001$), we used the residuals of the regression between body mass and horn length as a measure of horn length. Only body mass, however, affected social rank of yearling males and females ($F_{1,12} = 6.48$, $P = 0.03$, $R^2 = 0.35$; Fig. 3). Residual variation in horn length, after accounting for mass, had no effect on rank ($F_{1,12} = 2.95$, $P = 0.11$). Aggressiveness of adult females on yearlings of both sexes was independent of maternal characteristics (GLM model with maternal age, social rank and reproductive status; $F_{3,28} = 0.44$, $P = 0.73$).

For the social rank of 2-year-olds, we tested for the effects of maternal characteristics and FCP, using a GLM (with no random effect of year) including body mass, horn length and sex. Neither maternal characteristics nor FCP affected the social rank of 2-year-olds (all $P > 0.13$). Similarly, the aggressiveness of adult females towards 2-year-olds of both sexes was independent of maternal characteristics (GLM model with maternal age, social rank and reproductive status; $F_{3,28} = 1.75$, $P = 0.18$). As in yearlings, body mass of 2-year-olds was positively correlated to horn length ($r = 0.71$, $N = 93$, $P < 0.001$). Therefore, we

used the residuals of the regression of horn length on body mass as a measure of horn length. The final model included only sex ($F_{1,23} = 22.04$, $P < 0.0001$, $R^2 = 0.49$), with no effect of either mass ($F_{1,22} = 1.15$, $P = 0.29$) or of residual horn length ($F_{1,22} = 0.05$, $P = 0.82$). We could not test whether maternal rank affected the social rank of 2-year-olds because of the small sample size available ($N = 3$). We then examined a larger sample with a GLM to determine whether both residual horn length and body mass affected rank at 2 years of age. A model with sex ($F_{1,51} = 49.49$, $P < 0.0001$) and body mass ($F_{1,50} = 5.05$, $P = 0.03$) explained 52.2% of the variance in social rank (total model: $F_{2,50} = 27.27$, $P < 0.0001$, $R^2 = 0.52$; Fig. 3), with males being dominant over females and rank increasing with mass.

Combining males and females, social ranks at 1 and 2 years of age were not significantly correlated ($F_{1,10} = 4.4$, $P = 0.07$, $R^2 = 0.29$; Fig. 4a). For females, ranks at 2 and 3 years of age were positively correlated ($F_{1,24} = 6.0$, $P = 0.02$, $R^2 = 0.20$; Fig. 4b).

The apparent maternal age effects on mass and horn length of yearlings were not evident among 2-year-olds. To determine whether this result was due to size-dependent yearling survival, we tested the effects of maternal age, yearling body mass and yearling horn length on survival from 1 to 2 years of age in a multiple logistic regression, but none were significant (maternal age: $Wald_{1,54} = 0.26$, $P = 0.61$; yearling mass: $Wald_{1,54} = 0.002$, $P = 0.96$; horn length: $Wald_{1,54} = 0.12$, $P = 0.73$). Analysis of yearling survival including those with unknown mothers also failed to reveal any effects of either mass ($Wald_{1,105} = 0.99$, $P = 0.32$) or horn length ($Wald_{1,105} = 0.41$, $P = 0.52$).

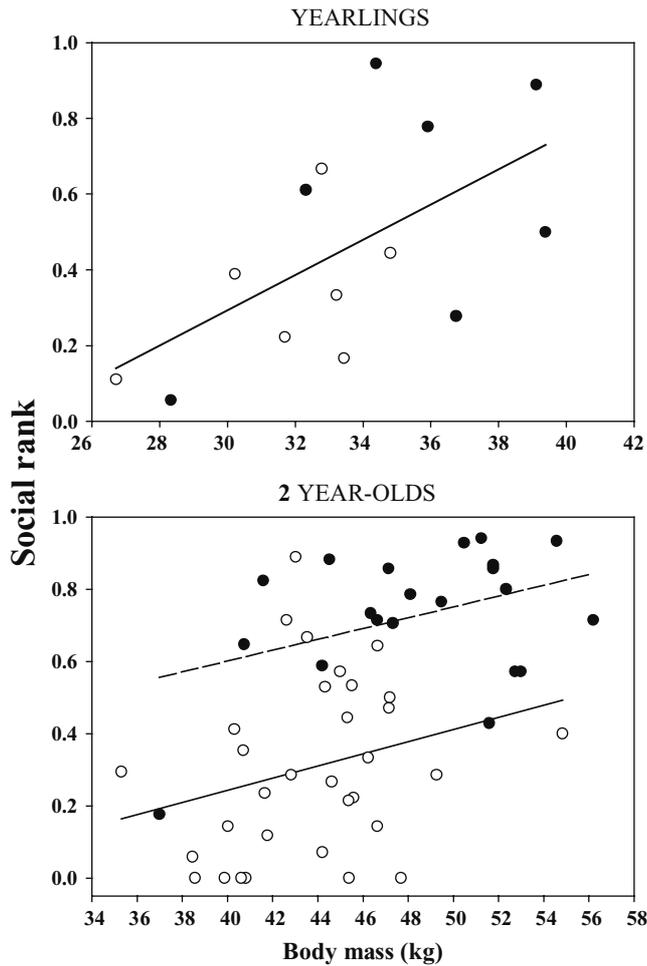


Fig. 3 Correlation between social rank and body mass in yearling and 2-year-old mountain goats at Caw Ridge, Alberta. Data for males (*solid circles*) and females (*open circles*) are shown for yearlings but the *solid line* refers to the regression analysis of the grouped data. For 2-year-olds, *open circles* and *solid line* = females, *solid circles* and *dashed line* = males

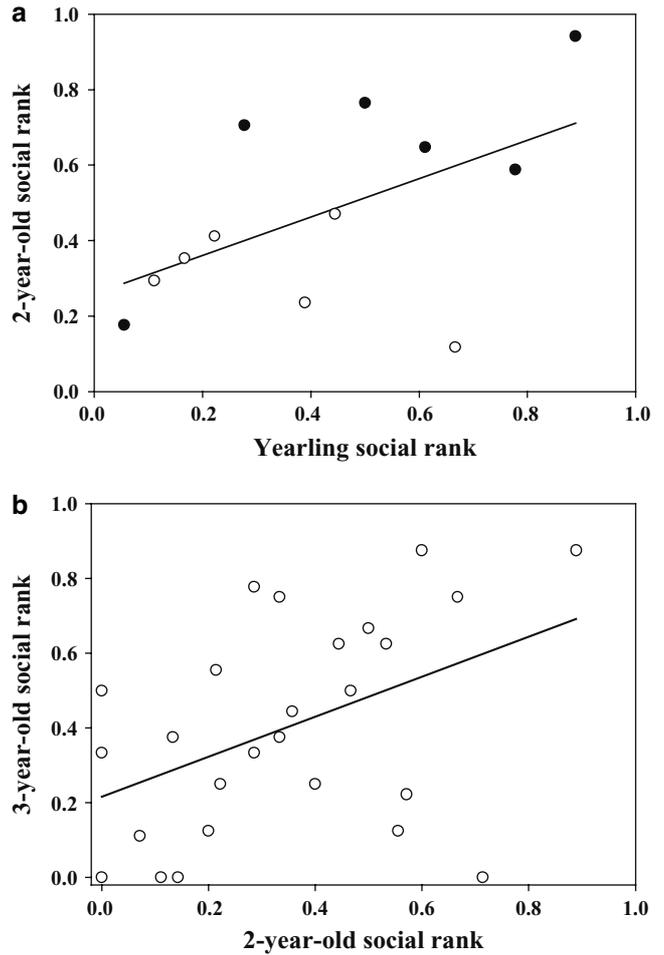


Fig. 4 Correlations of social rank in successive years in mountain goats. **a** Rank at 2 years of age as a function of yearling social rank. **b** Rank of females at 3 years of age as a function of social rank at 2 years of age. *Open circles* females, *solid circles* males

To test for possible compensatory growth between 1 and 2 years of age, we compared mass and horn length of yearlings to their gain in mass and horn length between 1 and 2 years. A GLMM with year ($N=11$) as a random term (variance explained by year was 55%) revealed no evidence of compensatory growth for horn length for either sex (all $P > 0.4$), but females showed compensatory growth in body mass between 1 and 2 years (interaction between mass and sex: $F_{2,32} = 4.88$, $P = 0.03$, total variance explained 88%; Fig. 5). The correlation of mass at 1 and 2 years of age was strong for males ($F_{1,20} = 26.35$, $P < 0.0001$, $R^2 = 0.57$) confirming the absence of compensatory growth, but not for females ($F_{1,22} = 2.57$, $P = 0.12$, $R^2 = 0.06$).

Discussion

Body mass of yearling males and horn length of yearlings of both sexes increased with maternal age. Social rank of yearlings also increased with their body mass. None of the maternal characteristics we examined affected

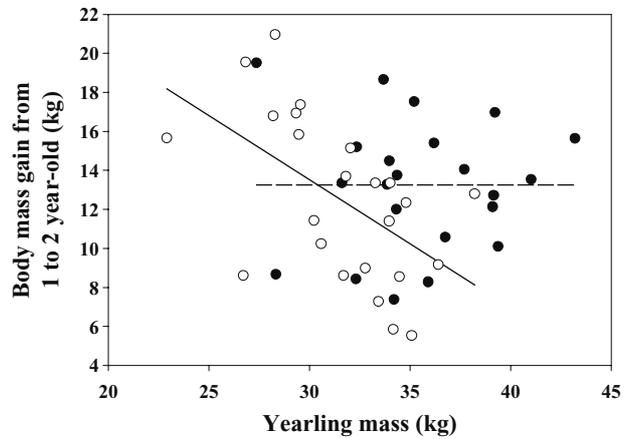


Fig. 5 Mass gain from 1 to 2 years of age in mountain goats at Caw Ridge, Alberta. Mass is adjusted to 15 July. *Open circles* and *solid line* = females; *solid circles* and *dashed line* = males

the development of 2-year-olds. Because the social rank established during the yearling year may persist into adulthood, however, maternal age may have a weak but persistent effect on mountain goats.

We could not establish whether the offspring of older mothers benefited from the greater experience or the better condition of their mothers, or a combination of the two. The relationship between maternal age and the body mass of yearling males appears to be due to a negative effect of very young mothers rather than to a positive effect of older mothers (Fig. 1). Mountain goat females complete body growth at 6 years (Côté and Festa-Bianchet 2003), and young mothers may face a trade-off between growth and reproduction, as suggested by Gallant et al. (2001) for bighorn sheep (*Ovis canadensis*). We found no indication that maternal senescence affected the growth of yearlings, because yearlings born to mothers older than 10 years were similar in mass and horn length to those born to mothers aged 7 to 9 years (Fig. 1). Thus, despite a small ($\approx 10\%$) but significant reduction in reproductive success in mothers ≥ 10 -years-old (Côté and Festa-Bianchet 2001a) and a decline in female survival after 9 years of age (Festa-Bianchet et al. 2003), the physical development of offspring of older mothers showed no evidence of either terminal investment or senescence.

Maternal age was positively related to yearling body mass in males but not in females, suggesting a sex bias in maternal care. Trivers and Willard (1973) predicted that mothers in good condition should invest more in the sex that can provide the greatest fitness returns. In polygynous and sexually dimorphic species such as mountain goats, male reproductive success generally depends upon body mass and fighting skills (Andersson 1994; Hewison and Gaillard 1999). A son that received a very high level of maternal care could potentially provide many grandchildren by monopolising access to oestrous females. In mountain goats, older mothers are heavier, dominant, and produce relatively more sons than younger mothers (Côté and Festa-Bianchet 2001c). Possibly, with increasing age, mothers increase the amount of care devoted to sons, but care devoted to daughters seems independent of maternal age. Mountain goats may fulfill the predictions of the Trivers-Willard hypothesis: high-quality (older) mothers produce more sons and maternal age is correlated with body mass for yearling sons but not for yearling daughters. Maternal age effects on yearling development may result mostly from a trade-off between growth and reproduction for young mothers, and suggest that young mothers may benefit from producing a female-biased offspring sex ratio (Côté and Festa-Bianchet 2001c). Differences in yearling body mass may play a more important role on future reproductive success for males than for females, because the post-weaning development of males appears to provide few opportunities for compensatory growth. Festa-Bianchet et al. (2000) found that mass during early development had a stronger effect on adult mass for male than for female bighorn sheep. Future research should examine the strength of the correlation between juvenile phenotype and adult phenotype and reproductive success.

Yearling horn length increased with maternal age for both sexes. In adult mountain goats, there is almost no

sexual dimorphism in horn length (Côté et al. 1998b), but dimorphism in mass is substantial (Côté and Festa-Bianchet 2003). It is reasonable, therefore, to suspect that variability in male reproductive success is affected by individual body mass more than by horn size (Geist 1964; Côté et al. 1998b). Female mountain goats interact aggressively with each other at a higher rate than most other female ungulates (Fournier and Festa-Bianchet 1995) and body mass or horn length may affect female social rank (Côté 2000). By affecting horn length, mother's age may have a positive effect on the social rank of juveniles.

Body mass of yearlings and 2-year-olds of both sexes was positively correlated with their social rank. Through its positive effect on body mass and horn development of yearling males, maternal age may affect adult social rank and possibly the reproductive success of sons. Despite the small sample, we found a correlation of 0.54 between social rank as a yearling and as a 2-year-old for both sexes. For females, ranks at 2 and at 3 years of age were correlated. The weak correlation between social ranks at 1 and 2 years of age could partly be explained by the compensatory growth observed in female mass. Because body mass and social rank in juvenile goats are correlated, differences in compensatory growth may result in changes in social rank of individual females between 1 and 2 years of age. Côté (2000) reported a strong year-to-year stability in social ranks of adult (≥ 3 years) females, with no effect of mass or horn length once age was accounted for. Because it appears to be independent of most adult physical characteristics, we suggest that adult female social rank within a cohort is established at a very early age, likely when females are 2 years old, and then persists into adulthood. An early establishment of female social rank has also been suggested for bighorn sheep (Festa-Bianchet 1991) and red deer (*Cervus elaphus*; Thouless and Guinness 1986).

Maternal effects are likely to weaken after the period of maternal care. The strength of maternal effects into adulthood should therefore increase with the proportion of body growth that occurs while receiving maternal care (Wolf et al. 1998). Two-year-old mountain goat females average about 65% of their asymptotic weight, while 2-year-old males only attain on average 52% of their adult weight (Côté and Festa-Bianchet 2003). Therefore, goats undergo a substantial amount of body growth after the period of maternal care, and events independent of maternal attributes may have a strong effect on their adult characteristics and therefore on their reproductive success. Some positive effects of maternal characteristics on juveniles, such as increased protection from predators (Côté et al. 1997), may also be difficult to detect. Even if we did not detect any effect of the mother-juvenile association on juvenile development (Tables 2 and 3), yearlings (65%) were associated with their mother much more often than 2-year-olds (8%). The potential for maternal effects through maternal care appears therefore much reduced for 2-year-olds compared to yearlings. Because our analyses suggested that maternal effects were no longer detectable at 2 years of age, we examined factors that may have affected our results, such as size-biased survival and compensatory growth between 1 and 2

years of age. Survival from 1 to 2 years of age was independent of mass as a yearling, and we only found compensatory growth for body mass of juvenile females. Therefore, maternal effects among 2-year-olds appear to be very weak.

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