Birthdate, mass and survival in mountain goat kids: Effects of maternal characteristics and forage quality

2 AUTHORS:

Steeve D Côté
Laval University
154 PUBLICATIONS   **3,316** CITATIONS

Marco Festa-Bianchet
Université de Sherbrooke
237 PUBLICATIONS   **10,177** CITATIONS

Steeve D. Côté · Marco Festa-Bianchet

Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality

Abstract In temperate environments, early-born ungulates may enjoy a longer growth period before winter, and so attain a higher body mass and an increased probability of survival compared to late-born ones. We assessed the effects of maternal characteristics, forage quality and population density on kid birthdate, mass and survival in a population of marked mountain goats (*Oreamnos americanus*) in Alberta. The duration and timing of the birth season were similar in all years. Births were highly synchronised: 80% of kids were born within 2 weeks of the first birth. Maternal age, maternal social rank and density did not affect kid birthdate or mass. Previous breeding experience was not related to kid birthdate, but kids born to pluriparous mothers were heavier during summer than kids born to primiparous mothers. Male and female kids had similar mass and accumulated mass linearly during summer. Early-born kids were heavier than late-born kids. Faecal crude protein (FCP) in late spring and maternal mass were positively related to kid mass. Survival to weaning appeared higher for males (90%) than for females (78%), but survival to 1 year was 65% for both sexes. FCP in late spring, density, birthdate and mass did not affect kid survival to weaning in either sex. Survival to 1 year increased with FCP in late spring for females, but not for males. Survival to 1 year was independent of birthdate for both sexes, but heavy females survived better than light ones. Multiple logistic regression revealed a positive effect of mass on survival to 1 year when the sexes were pooled. Our results suggest that mountain goats are constrained to give birth in a short birth season synchronised with forage productivity.

S.D. Côté (✉) · M. Festa-Bianchet
Groupe de recherche en écologie, nutrition et énergétique,
Département de biologie, Université de Sherbrooke, Sherbrooke,
PQ, J1K 2R1, Canada

S.D. Côté
Present address: Centre for Ecology and Hydrology,
Hill of Brathens, Banchory, Aberdeenshire, AB31 4BW,
UK, e-mail: s.cote@ceh.ac.uk,
Tel.: +44-1330-826333, Fax: +44-1330-823303

Introduction

Many animals have a short birth season, and birth synchrony could be a strategy to maximise fitness (Ims 1990). Highly synchronous birth seasons are typical of many ungulates, including gregarious bighorn sheep (*Ovis canadensis*: Festa-Bianchet 1988a), red deer (*Cervus elaphus*: Guinness et al. 1978a), wildebeest (*Conochaetes taurinus*: Estes 1976) and solitary species (moose, *Alces alces*: Bowyer et al. 1998; Keech et al. 2000; roe deer, *Capreolus capreolus*: Gaillard et al. 1993a; Linnell and Andersen 1998). Two non-exclusive hypotheses have been proposed to explain short parturition seasons in ungulates. First, the predator-satiation hypothesis suggests that offspring born during the birth peak have an increased chance of surviving the first critical weeks because of predator swamping (Dauphiné and McClure 1974; Estes 1976; Linnell et al. 1995). Alternatively, however, highly asynchronous births may reduce predation on neonates by making it unprofitable for a predator to switch from its regular prey species (Ims 1990). Second, the plant phenology hypothesis suggests that the timing of births affects offspring growth rate and consequently survival (Rutberg 1987). Parturition should occur just before the onset of vegetation growth, so that the high energetic demands of lactation will coincide with the greatest seasonal forage availability and quality, as well as relatively benign weather (Bunnell 1980, 1982; Thompson and Turner 1982; Rutberg 1984; Rachlow and Bowyer 1991).

Birthdate has important implications for various life history traits such as growth rate and survival. In temperate ungulates, access to high-quality vegetation for the longest possible period appears to be one of the main advantages enjoyed by early-born juveniles (Guinness et al. 1978b; Bunnell 1982; Festa-Bianchet 1988a; Linnell and Andersen 1998). Birthweight tended to decrease as the

fawning season progressed in pronghorn (*Antilocapra americana*) (Fairbanks 1993), and early-born offspring survived better than late-born ones in several ungulates (Guinness et al. 1978b; Festa-Bianchet 1988a; Birgersson and Ekvall 1997; Keech et al. 2000). Female ungulates in poor body condition tend to give birth later than other females (Mitchell and Lincoln 1973; Clutton-Brock et al. 1986; Verme 1989; Berger 1992; Byers 1997). In fallow deer (*Dama dama*), birthdate determines the time available for growth and lactation, and thus weaning mass and overwinter survival (Birgersson and Ekvall 1997). Weaning mass is related to survival in several ungulates (Festa-Bianchet et al. 1997; Loison et al. 1999; Milner et al. 1999; Unsworth et al. 1999).

In polygynous mammals, male offspring are expected to be heavier than female offspring at weaning because juvenile mass may have a stronger effect on the reproductive success of males than of females (Trivers and Willard 1973; Clutton-Brock et al. 1986). Birthdate and mass, therefore, could each affect the survival of offspring, either independently or interactively (Fairbanks 1993). Differences in juvenile survival are the major source of variation in lifetime reproductive success of female ungulates (Clutton-Brock 1988), and may be a major determinant of changes in population size (Gaillard et al. 1998).

Here we analyse how environmental and maternal characteristics affect survival of juvenile mountain goats (*Oreamnos americanus*). Because adult mountain goats are sexually dimorphic, with males weighing >40% more than females (Houston et al. 1989; Côté 1999), we expected that male kids would be heavier than female kids. Mountain goats live in very seasonal environments where late springs with deep snow cover until mid-June are not uncommon. Goat kids are of the 'montane follower' type (Geist 1981), capable of following their mother within 2–3 days of birth. Usually, the female and her newborn hide in rugged terrain such as cliff faces for a few days, before joining a nursery group. The proximity of escape terrain provides the main protection against predators, and nursery groups rarely wander away from cliff faces or steep rocky slopes. In this study, we first determined whether maternal characteristics such as age, previous breeding experience and social rank, and yearly differences in vegetation quality and population density affected kid birthdate, mass and survival. We then exam-

ined whether birthdate affected kid mass and survival, and assessed whether kid survival and growth patterns differed according to sex.

Materials and methods

We studied mountain goats at Caw Ridge (54° N, 119° W) in west-central Alberta (Canada) in the front range of the Rocky Mountains. The mountain goat population used about 28 km² of alpine tundra and open subalpine spruce (*Picea engelmanii*) forest at about 2,000 m elevation. The climate is subarctic-arctic with long winters and short cool summers. Snowfalls can occur during any month. During our study, the average minimum and maximum daily temperatures in April, May and June were –6 and 1°C, –2 and 6°C, and 2 and 10°C, respectively. Precipitation during the vegetation growing season averaged 290±34 (SE) mm and ranged from 178 to 440 mm (Côté et al. 1998b). Meteorological data were recorded at #8 Mine of Smoky River Coal Limited, about 17 km from Caw Ridge at an elevation of 1,525 m.

Goats have not been hunted at Caw Ridge since 1969 and the population ranged from 76 to 114 individuals during our study. During June–September 1987–1997, we marked and measured 207 goats, captured in traps baited with salt. We immobilised adult goats with xylazine hydrochloride, whose effect was reversed by injection of idazoxan (Haviernick et al. 1998). Captured kids were not drugged and survival did not differ between marked and uncaptured kids (Côté et al. 1998a). We marked kids with small Allflex plastic ear tags and adults with canvas collars or ear tags. Côté et al. (1998a) provide further details on capture procedures.

For goats first caught as adults, age was determined by counting the number of horn annuli, a technique reliable up to 7 years of age (Brandborg 1955; Stevens and Houston 1989; Côté et al. 1998b). The exact age was known for 51 adult females (86.4% of those studied) and estimated for 8 females first caught when ≥7 years old. We weighed goats to the nearest 0.5 kg with a spring scale hung from a tripod. Kids were captured and weighed only once during the summer. Our sample of body mass for adult females is small because we caught few females after 1993, when we determined that there was an increased risk of kid abandonment by handled females (Côté et al. 1998a). We excluded all abandoned kids from the data set because abandonment decreased kid survival (Côté et al. 1998a).

We used spotting scopes (×15–×45) 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 whether marked females were lactating, by direct observations of nursing behaviour. From mid-May to early June 1993–1997, we searched the study area intensively and attempted to observe as many adult females as possible each day. Less intensive observations were conducted during the parturition season in 1991 and 1992. Two known cases of twinning (0.8% of all births) were excluded from the data set. Unmarked kids were sexed by observation of the vulvar patch in females and by their urination posture.

Table 1 Descriptive statistics of the birth season of mountain goats at Caw Ridge, Alberta

Year	Birthdate		First kid	Last kid	Length of the birth season (days)	80% of births[a]		Number of kids with known birthdate each year
	Mean	Median				Date	Number of days	
1993	1 June	27 May	19 May	03 July	47	07 June	19	14
1994	28 May	24 May	21 May	19 June	28	02 June	11	23
1995	29 May	27 May	22 May	26 June	34	03 June	11	28
1996	28 May	25 May	20 May	24 June	34	02 June	12	21
1997	26 May	24 May	20 May	16 June	26	27 May	7	23
1993–1997	28 May	26 May	19 May	03 July	34	01 June	13	109

[a] Date by which 80% of the kids were born and number of days from first birth to when 80% of the kids were born

We determined kid birthdate ±1 day by direct observation for 77% of 124 kids born during our study. When we knew the kid birthdate ±5 days (based on the characteristics of the umbilical cord and a comparison of the kid's behaviour and body size with known-age kids), we used the median date. When the accuracy of our estimate was more than ±5 days, the kid was not assigned a birthdate. For each year from 1993 to 1997, we determined the total length of the parturition season (days from first to last birth) and the number of days from first birth to the 80th percentile of births (Rutberg 1987). The latter measure (80% of births) represents the period when the majority of births occur, is not affected by the timing of a few late births, and has often been used as a measure of the birth season for ungulates (Rutberg 1984, 1987; Berger 1992).

We determined kid survival to weaning by noting which marked females were accompanied by a kid on 15 September. We defined mid-September as the time of weaning because kids whose mother died in autumn were capable of surviving the winter (see Results). We assessed overwinter survival by determining which kids survived to 1 June. We are confident of our survival estimates because no marked kid was ever missed as a yearling and subsequently sighted, and all females and juveniles were seen >30 times each summer. In addition, emigration was very rare in our study population and never occurred before 2 years of age (Côté 1999).

We collected fresh groups of faecal pellets from 1990 to 1997. Pellets were dried and analysed for crude protein content with the macro-Kjeldhal acid digestion technique (Association of Official Analytical Chemists 1980). Faecal crude protein is a reliable indicator of forage quality (O'Donovan et al. 1963; Festa-Bianchet 1988b) and has often been used in the study of wild ungulates (Leslie and Starkey 1985; Festa-Bianchet 1988b). Annual variations in faecal crude protein are likely due to differences in weather, particularly temperature and the duration of snow cover. We determined faecal crude protein just after the peak parturition period (1 June±2 days; Table 1) because late spring appears to be a crucial period for the nutrition of lactating females (Portier et al. 1998).

From 1994 to 1997, we recorded agonistic encounters between adult female goats using all-occurences sampling and focal observations (Altmann 1974). The identity of initiator, winner and loser was noted for each interaction. We excluded aggressive encounters recorded at the trap site (Côté 2000). From 1994 to 1997, we ordered adult females in annual hierarchies that were most consistent with a linear hierarchy according to de Vries (1998), using Matman 1.0 for Windows (Noldus Information Technology 1998; Côté, in press a). The dominance hierarchy was reorganised by an iterative procedure that minimised inconsistencies. Because matrix size varied from 38 females in 1994 to 45 in 1997, we transformed social ranks according to the formula $1-rank/N_i$ where N_i is the number of adult females during year i. Social ranks therefore varied from 0 (subordinate) to 1 (dominant). Because the probability of winning an encounter and social rank are strongly related to age (>94% of interactions are won by the older female; Côté, in press a), we used the age-corrected residuals of social rank in the analyses.

Statistical analyses

We used multiple regression to assess the effects of faecal crude protein in late spring, maternal age, previous breeding experience, maternal social rank and density on kid birthdate and mass. Similarly, we used multiple logistic regression to determine the effects of faecal crude protein, kid birthdate, kid mass and density on the probability of kid survival. We used the backward stepwise procedure with the log-likelihood ratio and the criteria α=0.05 to enter and α=0.10 to remove in SPSS 8.0 for Windows. Birthdate was ln-transformed to meet normality and we used 15 September as the approximate date of weaning. We adjusted mass of females to mid-summer (15 July) using the average summer mass accumulation rate for adult females (Côté et al. 1998a). Because the sexes are segregated during most of the year, density was defined as the number of females at least 2 years old in the population on 1 June and ranged from 40 to 54 during the study. A similar measure of population density has been used in other ungulate studies (Festa-Bianchet et al. 1997; Kruuk et al. 1999).

Results

Birthdate

From 1993 to 1997, the median birthdate did not vary statistically, but ranged from 24 to 27 May (Table 1; ANOVA year effect on birthdate: $F_{4,104}=1.48$, $P=0.2$). The first birth observed each year occurred between 19 and 22 May (Table 1). Most kids (80%) were born within 2 weeks of the first birth (Table 1, Fig. 1). Parturitions were therefore highly synchronised and <20% of kids were born later than 1 June (Table 1, Fig. 1). The entire parturition season lasted 34 days on average (Table 1). The mean birthdate of both male ($n=58$) and female ($n=59$) kids from 1991 to 1997 was 28 May.

We assessed the effects of maternal age, social rank, previous breeding experience (primiparous vs multiparous) and density on kid birthdate. The model with all covariates explained very little of the variance in birthdate and was not significant ($F_{4,87}=0.61$, $P=0.7$, $R^2=0.03$). The final model did not include any of the covariates (age: $P=1.0$, Fig. 2a; social rank: $P=0.2$, Fig. 2b; parity: $P=0.5$; density: $P=0.7$). Separating the analysis by kid sex produced similar results (males: $F_{4,39}=0.96$, $P=0.4$; females: $F_{4,38}=0.74$, $P=0.6$).

Kid mass

Kids gained mass linearly during summer, according to the equation: mass (kg)=0.197(days since 1 June)+4.843 ($F=400.5$, $P<0.0001$, $r^2=0.83$, $n=84$; Fig. 3). More than four-fifths of the variability in kid mass was explained by capture date. Using exact kid age rather than days after 1 June greatly reduced sample size but yielded similar results [mass=0.221(age in days)+3.236, $F=308.7$, $P<0.0001$, $r^2=0.87$, $n=49$]. Curvilinear regression did not explain significantly more variance ($P>0.05$). Male and female kids had similar mass (ANCOVA with date: sex,
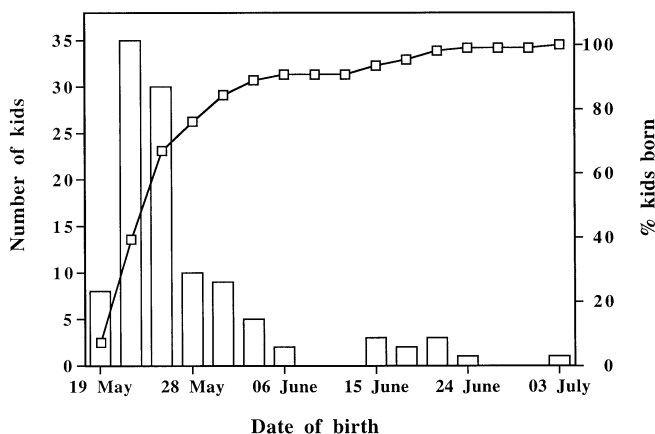

Fig. 1 Birthdates of 109 mountain goat kids in 1993–1997 at Caw Ridge, Alberta. *Histograms* indicate the number of kids born every 3 days beginning 15 May. The *solid line* shows the cumulative percentage of kids born
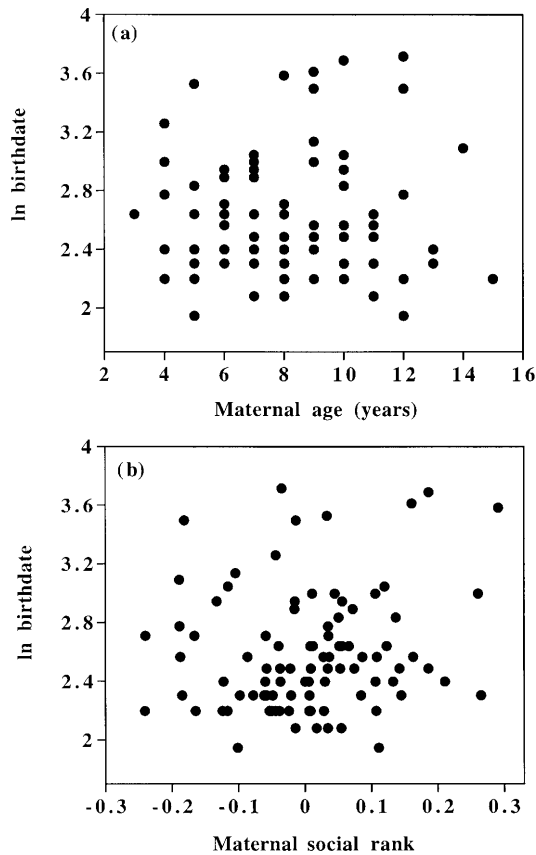
Fig. 2 Relationships between birthdate of mountain goat kids and maternal age (**a**) and age-corrected maternal social rank (**b**). Birthdate was ln-transformed to meet normality

Fig. 3 Summer mass gain by mountain goat kids at Caw Ridge, Alberta, 1988–1997. Males are indicated by *open circles* and *solid line*, females by *closed circles* and *dashed line*. Each point refers to an individual kid

Fig. 4 Residuals of kid mass on capture date according to percent faecal crude protein in late spring (1 June±2 days). Each *point* shows the average residual kid mass each year. Sample sizes from 1990 to 1997 were 11, 4, 11, 9, 5, 11, 9, and 14 kids

$F_{1,80}=0.78$, $P=0.4$; Fig. 3). Although growth rate appeared higher for males than females (225 vs 188 g/day; Fig. 3), the difference was not significant (ANCOVA: date×sex, $F_{1,80}=2.97$, $P=0.09$). We used the residuals of kid mass on capture date to account for mass gain during summer and found that kid mass varied among years (ANOVA: $F_{7,66}=3.48$, $P=0.003$; Fig. 4). Faecal crude protein in early June was correlated with the residuals of kid mass on capture date (linear regression: $F=17.49$, $P<0.0001$, $r^2=0.20$, $n=74$; Fig. 4). As predicted, the availability of high-quality vegetation appeared particularly important early in the season because faecal crude protein in July did not vary much among years (20–24%) and was not correlated with kid mass ($P=0.9$).

To further explore the factors affecting kid mass, we performed a multiple regression with maternal age, age-specific social rank, previous breeding experience, kid birthdate, faecal crude protein in late spring and density on the residuals of the linear regression of kid mass on capture date. Only birthdate ($B=-0.41$, $P=0.008$), faecal crude protein ($B=0.43$, $P=0.004$) and previous breeding experience ($B=0.27$, $P=0.06$) affected kid mass, explaining about 35% of the variance (final model: $F_{3,33}=5.99$, $P=0.002$; Figs. 4, 5a). Early-born kids were heavier than late-born ones when accounting for the effects of capture date on body mass (Fig. 5a). Kids born during years when faecal crude protein
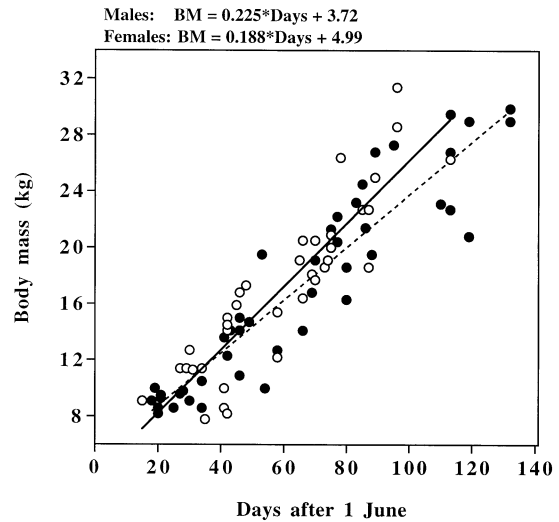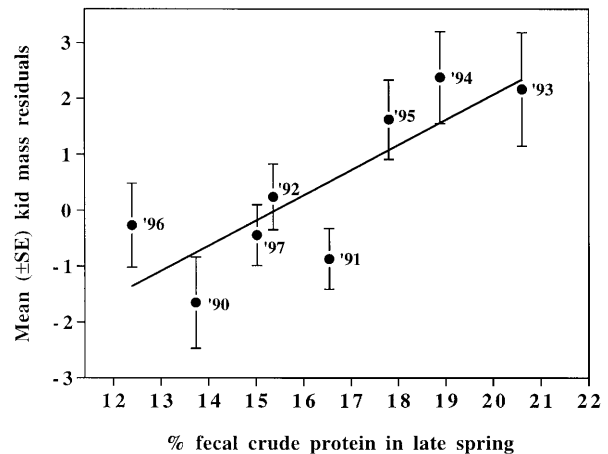
in late spring was high were heavier than kids born during bad years (Fig. 4). Multiparous mothers tended to have heavier kids than primiparous mothers, but the relationship was weak ($P=0.06$). Kid sex did not improve the model ($P=0.3$). We could not include maternal mass in this model because we only captured nine mothers during the period we studied social rank. However, over the entire study, the residuals of kid mass on capture date were positively correlated with maternal mass (linear regression: $F=6.23$, $P=0.02$, $r^2=0.17$; Fig. 5b).

Kid survival

Overall, kid survival was 78.5% to weaning and 60.3% to 1 year (Table 2). Survival to weaning appeared higher
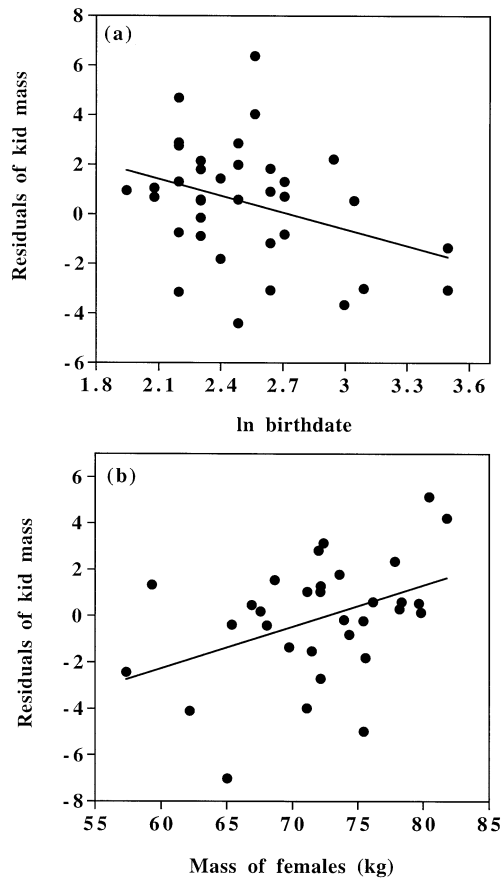
Fig. 5 Effect of birthdate (**a**) and maternal mass adjusted to 15 July (**b**) on mass of mountain goat kids at Caw Ridge, Alberta. We used the residuals of kid mass on capture date to account for mass gain during summer. Each *point* in (**b**) refers to a different mother

Table 2 Survival of mountain goat kids at Caw Ridge, Alberta, 1991–1997. Sample size for both sexes differs from the sum of males and females for kids who did not survive, because sex was unknown for some kids that died at a young age

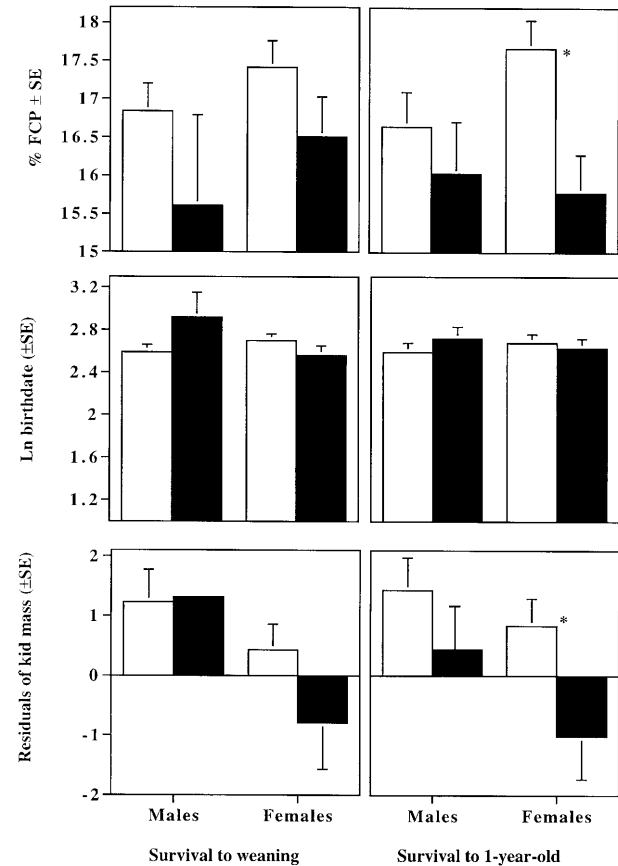| Sex	To weaning		To 1 year	
	Yes	No	Yes	No
Male	60 (89.6%)	7 (10.4%)	37 (64.9%)	20 (35.1%)
Female	57 (78.1%)	16 (21.9%)	42 (64.6%)	23 (35.4%)
Both	117 (78.5%)	32 (21.5%)	79 (60.3%)	52 (39.7%)

Fig. 6 Mean faecal crude protein (*FCP*) in late spring, birthdate and kid mass for mountain goat kids that survived (*white bars*) or not (*black bars*) to weaning and to 1 year at Caw Ridge, Alberta, 1991–1997. Birthdate was ln-transformed to meet normality. We used the residuals of kid mass on capture date to account for mass gain during summer. Sample sizes and statistics are presented in the text

for males than for females (89.6 vs 78.1%), but the difference was not significant (*G*-test: $G_1=3.44$, $P=0.07$; Table 2). Survival to 1 year was independent of sex ($G_1=0.001$, $P=1$; Table 2). Survival to 1 year of kids whose mother died overwinter (three out of nine survived) was not significantly lower than the survival of kids whose mother survived (Table 2; $G_1=2.87$, $P=0.09$), but the sample of orphans was very small. Only one of eight kids abandoned during summer survived to 1 year (Côté et al. 1998a).

Faecal crude protein in late spring did not affect kid survival to weaning (males: $t_{65}=-1.10$, $P=0.3$; females: $t_{71}=-1.26$, $P=0.2$; both sexes: $t_{147}=-1.07$, $P=0.3$; Fig. 6) and was not related to survival to 1 year in males ($t_{55}=-0.79$, $P=0.4$; Fig. 6). Female survival to 1 year, however, was positively correlated with faecal crude protein in late spring ($t_{63}=-3.07$, $P=0.003$; Fig. 6). Kid survival to weaning (males: $t_{54}=1.65$, $P=0.1$; females: $t_{56}=-1.10$, $P=0.3$; Fig. 6) and to 1 year (males: $t_{48}=0.86$, $P=0.4$; females: $t_{50}=-0.37$, $P=0.7$; Fig. 6) was independent of birthdate. Similarly, comparing the survival of kids born before and after 1 June did not reveal any effect of birthdate on survival to weaning (<1 June: 76% survived, $n=96$; ≥1 June: 80% survived, $n=25$; $G_1=0.18$,

$P=0.7$) or to 1 year (<1 June: 57% survived, $n=85$; ≥1 June: 54% survived; $n=24$; $G_1=0.04$, $P=0.8$). Survival to weaning did not vary with kid mass for either sex (males: $t_{25}=0.03$, $P=1.0$; females: $t_{29}=-1.05$, $P=0.3$; Fig. 6). Heavy kids were more likely to survive to 1 year than light kids, but the effect was weak (both sexes: $t_{52}=-1.98$, $P=0.05$; Fig. 6). The direction of the results was the same for both sexes, but the effect was only significant for females (males: $t_{23}=-1.03$, $P=0.3$; females:

Table 3 Logistic regression models of the effects of faecal crude protein (FCP) in late spring, birthdate, density and mass on the probability of survival for mountain goat kids at Caw Ridge, Alberta, 1991–1997. We conducted a backward stepwise regression on the residuals of kid mass on capture date to account for summer mass gain. Birthdate was ln-transformed to meet normality

		$B\pm$SE	R	P
Kid survival to weaning (n=46)				
Variables in the equation	Constant	2.35±0.52		<0.001
Variables not in the equation	FCP in late spring		0	0.2
	Ln(birthdate)		0	0.5
	Density		0.12	0.1
	Residuals of kid mass		0	0.5
Kid survival to 1 year (n=44)				
Variables in the equation	Constant	0.26±0.34		0.4
	Residuals of kid mass	0.30±0.15	0.17	0.05
Variables not in the equation	FCP in late spring		0	0.6
	Ln(birthdate)		0	0.5
	Density		0	0.3

$t_{27}=-2.13$, $P=0.04$; Fig. 6). We also used multiple logistic regression pooling the two sexes to test the effects of faecal crude protein in late spring, birthdate, density and residual mass on kid survival to weaning and to 1 year. This analysis confirmed that faecal crude protein in late spring, kid birthdate and the residuals of kid mass did not affect survival to weaning (Table 3). Faecal crude protein in late spring and kid birthdate were also not related to kid survival to 1 year (Table 3). The residuals of mass on capture date, however, affected the probability of survival to 1 year (Table 3), indicating that heavier kids survived better than light ones. Density did not affect survival to weaning or to 1 year (Table 3).

Discussion

Birthdate

Among temperate ungulates, the pattern of a sharp birth peak lasting 2–3 weeks is remarkably consistent between years and species (Guinness et al. 1978a; Rutberg 1984; Festa-Bianchet 1988a; Rachlow and Bowyer 1991; Fairbanks 1993; Gaillard et al. 1993a; Linnell and Andersen 1998). Mountain goats are no exception, and have a short birth pulse between 20 May and 3 June (Table 1, Fig. 1). Although the beginning of the birth season was highly synchronised, the temporal distribution of births was characterised by a long right tail with a few late births from mid-June to early July (Fig. 1). The gap in parturitions between 6 and 15 June may suggest that late births resulted from females that failed to conceive during their first oestrus.

Predation on newborns was unlikely to be a major selective force for the maintenance of highly synchronous parturitions, because 95% of kids survived to 2 weeks of age. Most kid mortality occurred during autumn (Festa-Bianchet et al. 1994). Similarly to bighorn sheep (Festa-Bianchet 1988a), mountain goat females gave birth in or near escape terrain that appeared relatively safe from predators, unlike the situation experienced by wildebeest (Estes 1976). In addition, female goats can defend their kids against predators in certain situations

(Côté et al. 1997). The most likely advantage of early birth is access to high-quality and abundant forage for the longest possible period, as suggested to explain the short lambing seasons of northern bighorn (Bunnell 1982; Thompson and Turner 1982; Festa-Bianchet 1988a) and Dall's sheep (*Ovis dalli*) (Rachlow and Bowyer 1991).

Contrary to our prediction, maternal age, social rank and previous breeding experience did not affect kid birthdate. Maternal effects, however, may be difficult to detect because of the short birth season. In ungulates, the effects of maternal characteristics on offspring birthdate vary among species, and no general pattern is evident. In some gregarious and solitary species, young and primiparous females tended to give birth later than mature females [bighorn sheep: Festa-Bianchet 1988c; mouflon (*Ovis gmelini*): Bon et al. 1993; red deer: Mitchell and Lincoln 1973; white-tailed deer (*Odocoileus virginianus*): Verme 1989], and dominant females gave birth earlier than subordinates in red deer (Clutton-Brock et al. 1986) and pronghorn (Byers 1997). In other species, however, birthdate was independent of maternal age (Green and Rothstein 1991; Byers 1997; Linnell and Andersen 1998) or social rank (Hass 1991; Green and Rothstein 1991).

Kid mass

The linear growth rate of mountain goat kids during summer was similar to that observed in other ungulates (Gaillard et al. 1993b; Festa-Bianchet et al. 1996). The absence of a significant sex difference in kid mass, however, was surprising. Because mountain goats are polygynous and adult males are >40% heavier than adult females (Houston et al. 1989), we expected that male kids would be heavier than female kids, as in other polygynous ungulates (Festa-Bianchet et al. 1996; Birgersson and Ekvall 1997; Loison et al. 1999). Sexual dimorphism develops very slowly in mountain goats, from non-significant at weaning to >40% at 6 years (Côté 1999). Because male and female kids have similar mass and growth rate during summer, there may not be any differential maternal investment in the sexes, in contrast to

other sexually dimorphic ungulates (Clutton-Brock et al. 1982; Bérubé et al. 1996; Birgersson et al. 1998).

Environmental conditions during the year of birth affect body growth and size in other ungulates (Albon et al. 1987; Gaillard et al. 1993b; Loison et al. 1999). Kid mass appeared to be partly determined by vegetation quality during early lactation (Fig. 6), but was not affected by population density. Because the timing of birth did not vary among years in our study, kids born in good years were relatively heavier during summer than kids born in poor years. During good years, the quantity or the quality of milk may increase because mothers have access to forage of higher protein content and digestibility than during poor years.

Birthdate affected kid mass during summer, probably because early-born kids, relative to late-born kids, enjoyed a longer growing period and benefited from milk of mothers foraging on more nutritious vegetation (Bunnell 1982; Rutberg 1987). Because maternal age and rank affected offspring mass in some ungulates (Clutton-Brock et al. 1984a, 1984b; Meikle et al. 1996; Kojola 1997), we predicted that old and dominant mothers would produce heavier kids than young and subordinate females. Although maternal age per se and social rank did not affect kid mass, multiparous and heavier mothers produced heavier kids (Fig. 5b), suggesting that large and experienced mothers may provide more maternal care than light and primiparous mothers. Although we could not rule out genetic effects, other studies of ungulates have found low heritabilities of juvenile mass (Réale et al. 1999). Maternal mass was strongly correlated with prewinter mass of fallow deer fawns (Birgersson and Ekvall 1997). In contrast, lamb mass at weaning was very weakly correlated with maternal mass in bighorn sheep (Festa-Bianchet and Jorgenson 1998).

Relative maternal investment may differ between species because of distinct strategies of acquisition and allocation of resources. At one end of the spectrum, individuals may rely on stored resources to sustain the costs of reproduction (capital breeders), while an alternative strategy is to use energy acquired during the reproductive period to offset reproductive costs (income breeders) (Jönsson 1997). Similar to bighorn sheep (Festa-Bianchet et al. 1996, 1998), mountain goat females show large seasonal and annual fluctuations in body mass and store substantial amounts of fat during the short growing season (Côté 1999). In contrast, other female ungulates such as roe deer may maintain a similar body mass throughout most of their adult life (Andersen et al. 2000). Postnatal maternal effort in mountain goats (kid growth rate of ca 200 g/day for 70-kg females, Fig. 3; Côté 1999) appears low compared to other ungulates such as roe deer (245–440 g/day per litter for 25-kg does, Gaillard et al. 1993b; Andersen and Linnell 1997) or pronghorn (490 g/day per litter for 45-kg does; Byers 1997). According to body mass variations and reproductive effort, mountain goats seem to adopt a capital breeding strategy, similarly to bighorn sheep (Festa-Bianchet et al. 1998). When resources are abundant, mothers should provide adequate maternal care to their kid, but during difficult years, reproducing females are expected to favour their own survival over that of their kid (Festa-Bianchet and Jorgenson 1998). Because a female can reproduce for up to 10 years (Côté 1999) and kid survival is dependent on body mass and forage quality (Fig. 6), the safer strategy appears to minimise reproductive costs during difficult years while maximising survival in order to reproduce again in future years (Clutton-Brock 1991). In addition, mountain goats use alpine habitats near escape terrain, with short and unpredictable growing seasons. Habitat selection may therefore limit the energy acquisition of females during the period of greatest energy demand (Bon et al. 1995; Kohlmann et al. 1996) and select for the capital breeder strategy.

Kid survival

We expected that the survival of mountain goat kids would decrease with later birthdate and higher density, increase with body mass, increase with the quality of late spring vegetation as reflected by faecal crude protein, and be positively affected by maternal mass, age and social rank. Most of our predictions were confirmed but, surprisingly, birthdate had no effect on kid survival, despite affecting kid mass.

In many ungulates, survival to 1 year is independent of sex (bighorn sheep: Bérubé 1997; pronghorn: Fairbanks 1993; red deer: Guinness et al. 1978b; but see Clutton-Brock et al. 1985; roe deer: Wauters et al. 1995). In mountain goats, survival to 1 year was similar in both sexes and appeared uncorrelated with maternal phenotypic quality (Côté 1999; Côté and Festa-Bianchet, in press). The mother's presence during the first winter, however, seemed to increase the probability of kid survival. Vegetation quality in late spring was positively related to survival in females, but not in males (Fig. 6), suggesting that female survival was more closely linked than male survival to available resources. These results indicate that environmental conditions affected young females more than young males, possibly because mothers increased the amount of care provided to sons but not to daughters during poor years, partly buffering the effects of difficult environmental conditions for sons. The fate of males and females born in good and difficult years would have to be monitored to understand the different effects of environmental conditions on sex-specific survival.

Kid mass did not affect survival to weaning. Because we first captured kids in late June, when they were about 1 month old, we cannot exclude the possibility that kids that died very young were lighter than those that survived. For example, age-specific body mass of roe deer fawns that died between 10 and 35 days of age was lower than that of surviving fawns (Andersen and Linnell 1998). Survival to 1 year was weakly related to mass for female kids, but not for males (Fig. 6). This result agrees with the findings that survival was positively related to

faecal crude protein in late spring only for female kids, and that crude protein affected kid mass. In addition, when the sexes were pooled in a multiple logistic regression model, mass affected kid survival to 1 year, but faecal crude protein did not. The probability of surviving the winter was positively related to body mass in juveniles of both sexes in red deer (Guinness et al. 1978b; Loison et al. 1999) and mule deer (*Odocoileus hemionus*) (Unsworth et al. 1999), but in bighorn and Soay sheep, mass was related to overwinter survival only at high density (Festa-Bianchet et al. 1997; Milner et al. 1999). In our study, density did not influence juvenile survival, but varied little between years (see Materials and methods). Possibly, the effects of mass and birthdate on kid survival may be weak in our study population because the low density does not greatly constrain access to food resources.

In ungulates, late-born juveniles generally show higher mortality than those born early (Guinness et al. 1978b; Clutton-Brock et al. 1982; Festa-Bianchet 1988a; Birgersson and Ekvall 1997; Keech et al. 2000). Although some kids were born relatively late (Fig. 1), we did not detect any effect of birthdate on survival (Table 3, Fig. 6). Although we cannot exclude the possibility that birthdate could have long-term effects on other life history traits (Green and Rothstein 1993), our results suggest that the factors affecting survival of newborn ungulates may differ according to species, population or local resource abundance.

References

Albon SD, Clutton-Brock TH, Guinness FE (1987) Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. J Anim Ecol 56:69–81

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Andersen R, Linnell JDC (1997) Variation in maternal investment in a small cervid; the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. Oecologia 109:74–79

Andersen R, Linnell JDC (1998) Ecological correlates of mortality of roe deer fawns in a predator-free environment. Can J Zool 76:1217–1225

Andersen R, Gaillard JM, Linnell JDC, Duncan P (2000) Factors affecting maternal care in an income breeder, the European roe deer. J Anim Ecol 69:672–682

Association of Official Analytical Chemists (1980) Official methods of analysis. Association of Official Analytical Chemists, Washington, DC

Berger J (1992) Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. Ecology 73:323–329

Bérubé C (1997) Les stratégies d'adaptation vitale chez les brebis du mouflon d'Amérique (*Ovis canadensis*): la reproduction en fonction de l'âge. PhD thesis, Université de Sherbrooke

Bérubé CH, Festa-Bianchet M, Jorgenson JT (1996) Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. Behav Ecol 7:60–68

Birgersson B, Ekvall K (1997) Early growth in male and female fallow deer fawns. Behav Ecol 8:493–499

Birgersson B, Tillbom M, Ekvall K (1998) Male-biased investment in fallow deer: an experimental study. Anim Behav 56:301–307

Bon R, Dardaillon M, Estevez I (1993) Mating and lambing periods as related to age of female mouflon. J Mamm 74:752–757

Bon R, Joachim J, Maublanc ML (1995) Do lambs affect feeding habitat use by lactating female mouflons in spring in areas free of predators? J Zool 235:43–51

Bowyer RT, Ballenberghe V van, Kie JG (1998) Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. J Mamm 79:1332–1344

Brandborg SM (1955) Life history and management of the mountain goat in Idaho. Idaho Wildl Bull 2:1–142

Bunnell FL (1980) Factors controlling lambing period of Dall's sheep. Can J Zool 58:1027–1031

Bunnell FL (1982) The lambing period of mountain sheep: synthesis, hypotheses, and tests. Can J Zool 60:1–14

Byers JA (1997) American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago

Clutton-Brock TH (ed) (1988) Reproductive success. University of Chicago Press, Chicago

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago

Clutton-Brock TH, Albon SD, Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308:358–360

Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133

Clutton-Brock TH, Albon SD, Guinness FE (1986) Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim Behav 34:460–471

Côté SD (1999) Dominance sociale et traits d'histoire de vie chez les femelles de la chèvre de montagne (in English). PhD thesis, Université de Sherbrooke

Côté SD (2000) Determining social rank in ungulates: a comparison of aggressive interactions recorded at a bait site and under natural conditions. Ethology 106:945-955

Côté SD (in press a) Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. Behaviour 137

Côté SD, Festa-Bianchet M (in press) Life-history correlates of horn asymmetry in mountain goats. J Mamm 82

Côté SD, Peracino A, Simard G (1997) Wolf, *Canis lupus*, predation and maternal defensive behavior in mountain goats, *Oreamnos americanus*. Can Field Nat 111:389–392

Côté SD, Festa-Bianchet M, Fournier F (1998a) Life-history effects of chemical immobilization and radiocollars on mountain goats. J Wildl Manage 62:745–752

Côté SD, Festa-Bianchet M, Smith KG (1998b) Horn growth in mountain goats (*Oreamnos americanus*). J Mamm 79:406–414

Dauphiné TC Jr, McClure RL (1974) Synchronous mating in barren-ground caribou. J Wildl Manage 38:54–66

Estes RD (1976) The significance of breeding synchrony in the wildebeest. East Afr Wildl J 14:135–152

Fairbanks WS (1993) Birthdate, birthweight, and survival in pronghorn fawns. J Mamm 74:129–135

Festa-Bianchet M (1988a) Birthdate and survival in bighorn lambs (*Ovis canadensis*). J Zool 214:653–661

Festa-Bianchet M (1988b) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586

Festa-Bianchet M (1988c) Age-specific reproduction of bighorn ewes in Alberta, Canada. J Mamm 69:157–160

Festa-Bianchet M, Jorgenson JT (1998) Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behav Ecol 9:144–150

Festa-Bianchet M, Urquhart M, Smith KG (1994) Mountain goat recruitment: kid production and survival to breeding age. Can J Zool 72:22–27

Festa-Bianchet M, Jorgenson JT, King WJ, Smith KG, Wishart WD (1996) The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. Can J Zool 74:330–342

Festa-Bianchet M, Jorgenson JT, Bérubé CH, Portier C, Wishart WD (1997) Body mass and survival of bighorn sheep. Can J Zool 75:1372–1379

Festa-Bianchet M, Gaillard JM, Jorgenson JT (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. Am Nat 152:367–379

Gaillard JM, Delorme D, Jullien JM, Tatin D (1993a) Timing and synchrony of births in roe deer. J Mamm 74:738–744

Gaillard JM, Delorme D, Jullien JM (1993b) Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. Oecologia 94:57–61

Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol Evol 13:58–63

Geist V (1981) On the reproductive strategies in ungulates and some problems of adaptation. In: Scudder GGE, Reveal JL (eds) Evolution today. Proceedings of the Second International Congress of Systematic and Evolutionary Biology. Hunts Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburg, pp 111–132

Green WCH, Rothstein A (1991) Sex bias or equal opportunity? Patterns of maternal investment in bison. Behav Ecol Sociobiol 29:373–384

Green WCH, Rothstein A (1993) Persistent influences of birth date on dominance, growth and reproductive success in bison. J Zool 230:177–186

Guinness FE, Gibson RM, Clutton-Brock TH (1978a) Calving times of red deer (*Cervus elaphus*) on Rhum. J Zool 185:105–114

Guinness FE, Clutton-Brock TH, Albon SD (1978b) Factors affecting calf mortality in red deer (*Cervus elaphus*). J Anim Ecol 47:817–832

Hass CC (1991) Social status in female bighorn sheep (*Ovis canadensis*): expression, development and reproductive correlates. J Zool 225:509–523

Haviernick M, Côté SD, Festa-Bianchet M (1998) Immobilization of mountain goats with xylazine and reversal with idazoxan. J Wildl Dis 34:342–347

Houston DB, Robbins CT, Stevens V (1989) Growth in wild and captive mountain goats. J Mamm 70:412–416

Ims RA (1990) The ecology and evolution of reproductive synchrony. Trends Ecol Evol 5:135–140

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66

Keech MA, Bowyer RT, Ver Hoef JM, Boertje RD, Dale BW, Stephenson TR (2000) Life-history consequences of maternal condition in Alaskan moose. J Wildl Manage 64:450–462

Kohlmann SG, Müller DM, Alkon PU (1996) Antipredator constraints on lactating Nubian ibexes. J Mamm 77:1122–1131

Kojola I (1997) Behavioural correlates of female social status and birth mass of male and female calves in reindeer. Ethology 103:809–814

Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE (1999) Population density affects sex ratio variation in red deer. Nature 399:459–461

Leslie DM, Starkey EE (1985) Fecal indices to dietary quality of cervids in old-growth forests. J Wildl Manage 49:142–145

Linnell JDC, Andersen R (1998) Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*. J Zool 244:497–504

Linnell JDC, Aanes R, Andersen R (1995) Who killed bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildl Biol 1:209–223

Loison A, Langvatn R, Solberg EJ (1999) Body mass and winter mortality in red deer calves: disentangling sex and climate effects. Ecography 22:20–30

Meikle DB, Drickamer LC, Vessey SH, Arthur RD, Rosenthal TL (1996) Dominance rank and parental investment in swine (*Sus scrofa domesticus*). Ethology 102:969–978

Milner JM, Albon SD, Illius AW, Pemberton JM, Clutton-Brock TH (1999) Repeated selection of morphometric traits in the Soay sheep on St Kilda. J Anim Ecol 68:472–488

Mitchell B, Lincoln GA (1973) Conception dates in relation to age and condition in two populations of red deer in Scotland. J Zool 171:141–152

Noldus Information Technology (1998) Matman, reference manual, version 1.0 for Windows. Wageningen, The Netherlands

O'Donovan PB, Barnes RF, Plumlee MP, Mott OG, Packett LV (1963) Fecal nitrogen indicator technique for determining the nutritive value of reed canarygrass. J Anim Sci 22:1144–1152

Portier C, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Yoccoz NG (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). J Zool 245:271–278

Rachlow JL, Bowyer RT (1991) Interannual variation in timing and synchrony of parturition in Dall's sheep. J Mamm 72:487–492

Réale D, Festa-Bianchet M, Jorgenson JT (1999) Heritability of body mass varies with age and season in wild bighorn sheep. Heredity 83:526–532

Rutberg AT (1984) Birth synchrony in American bison (*Bison bison*): response to predation or season? J Mamm 65:418–423

Rutberg AT (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. Am Nat 130:692–710

Stevens V, Houston DB (1989) Reliability of age determination of mountain goats. Wildl Soc Bull 17:72–74

Thompson RW, Turner JC (1982) Temporal geographic variation in the lambing season of bighorn sheep. Can J Zool 60:1781–1793

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Unsworth JW, Pac DF, White GC, Bartmann RM (1999) Mule deer survival in Colorado, Idaho, and Montana. J Wildl Manage 63:315–326

Verme LJ (1989) Maternal investment in white-tailed deer. J Mamm 70:438–442

Vries H de (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav 55:827–843

Wauters LA, Crombrugghe SA de, Nour N, Matthysen E (1995) Do female roe deer in good condition produce more sons than daughters. Behav Ecol Sociobiol 37:189–193