

# Is mother condition related to offspring condition in migratory caribou (*Rangifer tarandus*) at calving and weaning?

J. Taillon, V. Brodeur, M. Festa-Bianchet, and S.D. Côté

**Abstract:** Maternal characteristics can affect offspring traits, yet they are seldom included when considering density dependence of juvenile traits and population dynamics. We quantified the influence of population size and maternal traits on body condition of migratory caribou (*Rangifer tarandus* (L., 1758)) calves at birth and weaning. We contrasted female–calf pairs of the Rivière-George (RG) herd, which has recently declined to low population size, with pairs of the much larger Rivière-aux-Feuilles (RAF) herd. Calves of the RAF herd were lighter, smaller, and leaner than calves of the RG herd at both birth and weaning. Differences between herds, however, were much greater at weaning than at calving, suggesting a combined effect of herd size and summer range conditions on calf growth. Maternal mass was positively related to calf body condition during both periods. The positive influence of maternal mass on calf body condition was greater for RAF than RG calves at birth, but it was similar for the two herds at weaning. Our results show that the negative effect of population size on calf body condition can be modulated by maternal mass at calving, and that the positive effect of maternal mass is greater at weaning.

**Key words:** population size, maternal traits, juvenile body condition, calving, weaning, migratory caribou, *Rangifer tarandus*.

**Résumé :** Les caractéristiques maternelles peuvent influencer les traits de leur progéniture, mais sont rarement considérées lors de l'étude des effets de la densité sur les traits des juvéniles et la dynamique des populations. Nous avons évalué l'influence de la taille de population et des caractéristiques maternelles sur la condition physique des faons du caribou migrateur (*Rangifer tarandus* (L., 1758)) à la mise bas et au sevrage. Nous avons comparé des paires de femelle-faon du troupeau Rivière-George (RG) dont la taille de population a récemment décliné, à des paires du troupeau Rivière-aux-Feuilles (RAF) qui est présentement à taille de population élevée. Les faons du RAF présentaient une masse corporelle, une taille corporelle et un indice de gras des reins inférieurs aux faons du RG tant à la mise bas qu'au sevrage. Ces différences entre les troupeaux étaient plus importantes au sevrage qu'à la mise bas, suggérant un effet négatif combiné de la taille de population et des conditions d'alimentation estivale sur la croissance des faons. La masse maternelle était positivement corrélée à la masse des faons et ce, aux deux périodes. L'influence positive de la masse maternelle sur la masse du faon était plus forte pour le RAF que pour le RG à la naissance, mais semblable pour les deux troupeaux au sevrage. Nos résultats indiquent que l'effet négatif d'une taille de population élevée sur la condition corporelle des faons peut être modulé par la masse maternelle à la mise bas, et que cet effet positif de la masse maternelle est plus important au sevrage qu'à la mise bas.

**Mots-clés :** taille de population, caractéristiques maternelles, condition corporelle juvénile, mise bas, sevrage, caribou migrateur, *Rangifer tarandus*.

## Introduction

Population growth often depends on the combined effects of weather and density on the body condition, growth, reproduction, and survival of individuals (Clutton-Brock et al. 1985; Forchhammer et al. 1998; Gaillard et al. 1998; Post and Stenseth 1999). Weather may directly affect individuals through the energy costs of thermoregulation or movements

(Coulson et al. 2000; Mysterud and Ostbye 2006), and indirectly by affecting availability of resources (Langvatn et al. 1996; Owen-Smith and Mason 2005). For example, late snowmelt may delay access to spring forage, shorten the period when high-quality forage is available, and reduce body mass gain, gestation rate, and juvenile survival (Clutton-Brock and Coulson 2002; Mysterud and Ostbye 2006; Pettorelli et al. 2007). In addition to weather, population density

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often determines the amount of resources available per capita, affecting body condition, reproduction, and survival (Côté et al. 2004; Kjellander et al. 2006; Bonenfant et al. 2009).

The impact of population density on life-history traits may vary with season and sex – age class (Toïgo et al. 2006; Simard et al. 2008; Bonenfant et al. 2009). In ungulates, juveniles are more sensitive than adults to changes in density (Gaillard et al. 2000; Festa-Bianchet et al. 2003; Bonenfant et al. 2009). Juveniles born at high density may have lighter birth mass (Skogland 1983; Kjellander et al. 2006), lower growth rate (Hewison et al. 2002), or higher mortality (Owen-Smith 1990; Festa-Bianchet et al. 1998) compared with those born at low density. Density-dependent effects on juvenile body condition may persist into adulthood (Forchhammer et al. 2001; Pettorelli et al. 2002; Gaillard et al. 2003) and delay primiparity (Festa-Bianchet et al. 1995; Langvatn et al. 1996). Recently, Bonenfant et al. (2009) suggested that density dependence mostly affects demographic parameters through its impact on individual body condition. Changes in body condition of juveniles over time could therefore provide clues on the link between habitat quality and population dynamics.

In addition to environmental conditions, maternal characteristics also affect offspring body condition, growth, and survival (Festa-Bianchet 1988; Rönnegård et al. 2002; Hamel et al. 2009a, 2009b). Female ungulates in good body condition are more likely to reproduce (Cameron et al. 1993; Festa-Bianchet et al. 1998; Testa and Adams 1998) and tend to produce heavier offspring (Keech et al. 2000; Côté and Festa-Bianchet 2001) than females in poor body condition. Female age may also influence offspring survival, as young females tend to give birth later and produce lighter offspring than prime-aged females (Festa-Bianchet 1988; Verme 1989; Adams 2005).

Maternal effects may vary according to season and offspring age. During periods of high energetic demands, such as late gestation and early lactation (Ofteidal 1984; White and Luick 1984), maternal traits may have stronger effects on offspring development than at other times. Maternal effects should be stronger at birth and during growth, and usually weaken with offspring age (Wilson and Festa-Bianchet 2009). In temperate and arctic environments, parturition usually occurs just before spring green-up (Côté and Festa-Bianchet 2001; Post et al. 2003), and females partly rely on body reserves to provide maternal care (Crête and Huot 1993; Barboza and Parker 2008). Females also depend on available forage to sustain offspring growth from late gestation to weaning. Consequently, poor weather or high density that reduce food availability to mothers may lower newborn survival (Post and Klein 1999; Griffith et al. 2002), as well as growth and body condition at weaning (Clutton-Brock et al. 1987; Therrien et al. 2007). Despite strong evidence that maternal traits affect juvenile life-history traits (Wilson and Festa-Bianchet 2009), however, maternal traits are rarely considered in studies investigating the effects of density dependence on juvenile traits and population dynamics.

Here, we quantified the influence of population size and maternal traits on body condition of migratory caribou (*Rangifer tarandus* (L., 1758)) calves at birth and at weaning. We compared two herds with large and contrasting fluctuations in population size during recent decades. At both calving

and weaning, we expected that offspring condition would be influenced by an interaction between maternal traits and population size. We predicted that the positive relationship between the body condition of a female and that of her calf should be much stronger at high than at low population size, reflecting the effect of environmental factors on maternal condition and hence on offspring phenotype (Wilson and Festa-Bianchet 2009). We also expected that maternal traits would better predict offspring condition at weaning than at calving, reflecting the higher energetic costs of lactation compared with parturition. The comparison of calving and weaning will provide direct information on body condition and indirect information on the quality of the summer range of each herd. We also tested whether the effect of population size on calf body condition could be modulated by maternal mass so that this effect may vary during the reproductive cycle.

## Materials and methods

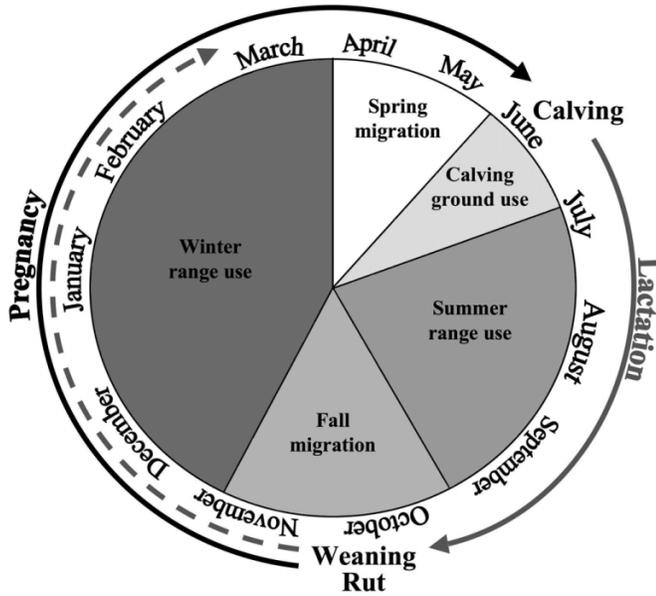
### Study area

In northern Quebec and Labrador, the Rivière-George (RG) and the Rivière-aux-Feuilles (RAF) caribou herds range over nearly 1 000 000 km<sup>2</sup> (Boulet et al. 2007). The two herds are not genetically different (Boulet et al. 2007), but they have shown largely independent fluctuations in size, recruitment rates, and individual body condition over the last few decades (Couturier et al. 2010). The RG herd increased from about 5 000 individuals in the 1950s (Banfield and Tener 1958) to more than 775 000 individuals in 1993 (Couturier et al. 1996), then declined to approximately 385 000 in 2001 (Couturier et al. 2004) and 74 000 in 2010 (Quebec Government aerial count). The RAF herd increased from 56 000 caribou in 1975 (Le Hénaff 1976) to 1 193 000 in 2001 (Couturier et al. 2004) and was estimated at 430 000 in 2011 (Quebec Government aerial count).

### Range use

For caribou, early-spring migration is usually associated with calving (Fig. 1), a period of high energetic requirements for females and high vulnerability to predation for newborns. At calving, females of the RG herd aggregate on high tundra plateaus on the east side of the Quebec–Labrador Peninsula (57°N, 65°W), while females of the RAF herd calve in the Ungava Peninsula (61°N, 74°W). Females are highly philopatric and over 93% return to their traditional calving grounds each year (Boulet et al. 2007). Females travel 250–650 km to reach calving grounds that are typically used from late May to early July (J. Taillon, M. Festa-Bianchet, and S.D. Côté, unpublished data). Summer ranges are larger than calving grounds and are used during lactation, from early July to mid-September. Migration from summer range to winter range occurs in early fall, at the time of physiological weaning and before the rut (Lavigne and Barrette 1992). The migration and seasonal ranges of caribou from the RG and RAF herds have been monitored since 1986 by an extensive survey of caribou fitted with radio collars (Couturier et al. 2004). There is no overlap in the calving grounds and summer ranges of the two herds (Couturier et al. 2004; Taillon et al. 2012).

**Fig. 1.** Annual range use and reproductive cycle of female migratory caribou (*Rangifer tarandus*). Estrus and conception occur during the fall rut, followed by pregnancy, calving, and lactation before the next rut (solid line) that can be extended (broken line).



### Body condition

At calving and weaning of 2007–2009, we collected mother–calf pairs of both herds (Table 1). At peak calving (6–14 June), we located caribou by helicopter. We collected mother–calf pairs over the entire calving grounds (calving ground size: RG = 6 500 ± 745 km<sup>2</sup>; RAF = 54 500 ± 2 700 km<sup>2</sup>) and collection sites were several kilometres apart (RG = 21 ± 3 km; RAF = 83 ± 12 km). Calves were reliably matched to females because mothers isolated themselves at parturition. Only females with a newborn calf (<2 days old) were sampled. Newborns were unsteady and unable to run, their hoof pads were barely worn, and the umbilical cord was still attached (Adams 2005; Couturier et al. 2009). At weaning (October–November; Table 1), groups of caribou were located from helicopter and mother–calf pairs were identified from behavioural observations on the ground. We collected pairs over the entire range covered by animals fitted with radio collars and spaced out collections by several kilometres (RG = 64 ± 9 km; RAF = 147 ± 27 km). Animals were culled to quantify body condition, parasite load, pathogens, contaminants, and heavy metals as part of ongoing studies on caribou biology and conservation (Ducrocq 2010; Taillon et al. 2011; J. Ducrocq, G. Beauchamp, S. Kutz, M. Simard, B. Elkin, B. Croft, J. Taillon, S.D. Côté, V. Brodeur, M. Campbell, D. Cooley, C. Cuyler, and S. Lair, unpublished data).

We collected the following measurements on females and calves: total mass (kg), hind-foot length (cm), and kidney fat (%). We estimated the age of females by counting cementum layers in incisor teeth (Hamlin et al. 2000) and noted the sex of calves. Mass of females was obtained using a spring scale (±0.25 kg). Most females were 4 years and older and their mass was not influenced by age (collinearity tests using variance inflation factors (VIF) and condition index (CI) were not significant (VIF < 10 and CI < 6); REG procedure in

**Table 1.** Sampling dates and sample size, by year and season, for mother–calf pairs of migratory caribou (*Rangifer tarandus*) from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, northern Quebec and Labrador, Canada.

Year	Season	Date of sampling	Pairs of female–calf ( <i>n</i> )	
			RG	RAF
2007	Calving	7–14 June	20	20
	Weaning	26 Oct. – 8 Nov.	18	19
2008	Calving	5–12 June	15	15
	Weaning	20 Oct. – 2 Nov.	15	15
2009	Calving	6–14 June	15	15
	Weaning	23–30 Oct.	15	15

SAS version 9.2 (SAS Institute Inc., Cary, North Carolina, USA); Belsley et al. 1980). Birth mass of calves was recorded to the nearest 0.1 kg using a Pesola spring scale (Pesola AG, Baar, Switzerland). Hind-foot length was measured from the calcaneum to the edge of the hoof (±0.2 cm) along the exterior of the foot. Kidney-fat index, the ratio of the mass of perinephric fat (±0.5 g; not including fat extending beyond the kidney; Riney 1960) and kidney mass (±0.5 g), was quantified as KFI = ((mass of fat around the kidneys) × (mass of kidneys without fat)<sup>-1</sup>) × 100 (Huot 1988). Animal manipulations followed guidelines of the Canadian Council on Animal Care; the Laval University Animal Care and Use Committee approved all procedures (#2008015-3).

### Statistical analyses

We tested the effects of year, herd, female age, body mass, hind-foot length, kidney fat, calf sex, and all second-degree interactions on calf mass, hind-foot length, and kidney fat (KFI) at calving and weaning separately, using multiple regression models in a distinct steps approach based on Hosmer and Lemeshow (2000). This approach considers possible correlations between covariates, reduces the number of explanatory variables tested in final models to avoid over-parameterization (remove variable with *P* > 0.20) and conserves degrees of freedom, before obtaining final regressions for each model. This technique also indicates the effect of each explanatory variable separately before considering them together. We selected the best model using a deletion *F* test that identifies, based on residual sums of squares, whether a more complex model is better ( $\alpha = 0.05$ ) or equivalent to a simpler model wherein a parameter(s) is removed (GLM-select procedure in SAS version 9.2; Crawley 2005). Explanatory variables selected from the deletion test procedure were included and tested in multiple regression models (GLM procedure in SAS version 9.2). We log-transformed calf mass and applied a square-root transformation to hind-foot and kidney-fat values to meet assumptions of normality and homogeneity of variance. The Hosmer and Lemeshow (2000) approach suggested that maternal mass explained more variability in calf measurements than female hind-foot length and kidney fat both at calving and weaning. Therefore, we present results only for the effect of maternal mass on calf mass, hind-foot length, and KFI. We also tested the effects of maternal age as a linear and a quadratic variable on calf measurements.

To compare the slopes of the relationships between maternal and calf mass between herds and between seasons, we

standardized variables (Schielzeth 2010). We used a *Z* test to compare slope estimates of the relationship between body mass of females and calves at calving and at weaning (lsmeans and SE produced by the regressions on standardized data). All data are presented as means  $\pm$  SE. A level of  $\alpha = 0.05$  was used to determine significance.

## Results

### Calving

We found no effects of year as a fixed effect (birth mass:  $F_{[2,99]} = 0.87$ ,  $P = 0.42$ ; hind-foot length:  $F_{[2,98]} = 0.94$ ,  $P = 0.39$ ; kidney fat:  $F_{[2,99]} = 2.33$ ,  $P = 0.10$ ) or in interaction with other factors (all  $P$  values  $>0.15$ ), indicating that factors influencing calf body condition at calving were similar over the study. Maternal age was unrelated to calf body condition (birth mass:  $F_{[1,94]} = 0.89$ ,  $P = 0.35$ ; hind-foot length:  $F_{[1,93]} = 0.82$ ,  $P = 0.37$ ; kidney fat:  $F_{[1,94]} = 0.01$ ,  $P = 0.93$ ). Age of 100 adult females collected at calving ranged from 2.5 to 12.5 years, and was similar between herds (RG =  $6.6 \pm 0.4$  years old; RAF =  $5.9 \pm 0.3$  years old;  $\chi^2_{[1,94]} = 1.75$ ,  $P = 0.19$ , Mann–Whitney *U* test) and among years ( $\chi^2_{[2,92]} = 0.70$ ,  $P = 0.71$ , Mann–Whitney *U* test).

Our final models explained, respectively, 41% of the variance in calf mass ( $F_{[5,94]} = 13.21$ ,  $P < 0.0001$ ), 27% in calf body size ( $F_{[4,94]} = 8.51$ ,  $P < 0.0001$ ), and 21% in calf KFI ( $F_{[1,98]} = 26.49$ ,  $P < 0.0001$ ) at calving (Table 2). RG newborns were heavier ( $6.05 \pm 0.13$  kg) and fatter ( $40.0\% \pm 1.6\%$  kidney fat) than RAF ones ( $5.35 \pm 0.12$  kg and  $28.9\% \pm 1.6\%$  kidney fat) (Table 2). There was, however, no difference in calf body size (hind-foot length: RG =  $33.3 \pm 0.2$  cm, RAF =  $33.0 \pm 0.2$  cm;  $t_{[1,98]} = 1.01$ ,  $P = 0.31$ ). We detected a positive effect of maternal mass on calf birth mass and body size: larger females produced larger calves (Table 2, Figs. 2a, 2b, calving). These positive relationships were stronger for RAF than RG for calf birth mass (RAF slope =  $0.07 \pm 0.02$ ,  $P < 0.0001$ ; RG slope =  $0.04 \pm 0.01$ ,  $P = 0.01$ ; comparison of slopes on standardized data:  $Z_{[1,49]} = 13.8$ ,  $P < 0.0001$ ) and calf body size (RAF slope =  $0.13 \pm 0.03$ ,  $P = 0.0001$ ; RG slope =  $0.02 \pm 0.03$ ,  $P = 0.40$ ; comparison of slopes on standardized data:  $Z_{[1,49]} = 16.2$ ,  $P < 0.0001$ ) (Table 2, Figs. 2a, 2b, calving). There was no effect of maternal mass on calf kidney fat ( $F_{[1,98]} = 0.44$ ,  $P = 0.51$ ) (Fig. 2c, calving).

Male calves were heavier (Table 2, Fig. 3a) and taller (hind-foot length:  $33.7 \pm 0.2$  cm) at birth than female calves (hind-foot length:  $32.7 \pm 0.2$  cm,  $t_{[1,98]} = 3.30$ ,  $P = 0.0014$ ). The nearly significant interaction between calf sex and herd on birth mass ( $F_{[1,94]} = 2.82$ ,  $P = 0.096$ ) suggested that sexual dimorphism at birth tended to be greater in the RG than in the RAF (Fig. 3a). Male calves of RG were heavier than females of RG ( $t_{[1,49]} = 3.96$ ,  $P = 0.0001$ ) and than males ( $t_{[1,38]} = 2.67$ ,  $P = 0.009$ ) or females of RAF ( $t_{[1,52]} = 4.63$ ,  $P < 0.0001$ ; Fig. 3a), whereas male calves of RAF had similar birth mass to females of both RG ( $t_{[1,46]} = 0.77$ ,  $P = 0.44$ ) and RAF ( $t_{[1,60]} = 1.50$ ,  $P = 0.14$ ) (Fig. 3a). There was no effect of calf sex on kidney fat ( $F_{[1,98]} = 2.91$ ,  $P = 0.09$ ).

### Weaning

Weaning mass varied among years (Table 2). Calves were

lighter in 2009 than in 2007 (difference of  $4.3 \pm 1.3$  kg,  $t_{[1,76]} = 3.43$ ,  $P = 0.0009$ ) and 2008 (difference of  $4.0 \pm 1.3$  kg,  $t_{[1,59]} = 3.05$ ,  $P = 0.003$ ). There was, however, no effect of year in interaction with other factors on body mass (all  $P$  values  $>0.15$ ) and no effect of year on calf body size ( $F_{[2,93]} = 2.79$ ,  $P = 0.08$ ) or body fat ( $F_{[2,94]} = 0.38$ ,  $P = 0.68$ ). Similar to calving, maternal age was unrelated to calf body condition in both herds (birth mass:  $F_{[1,93]} = 2.12$ ,  $P = 0.15$ ; hind-foot length:  $F_{[1,93]} = 0.74$ ,  $P = 0.39$ ; kidney fat:  $F_{[1,93]} = 0.04$ ,  $P = 0.84$ ). Ages of 97 females collected at weaning covered a wide range (2.5–13.5 years), and were similar between herds (RG =  $6.7 \pm 0.4$  years; RAF =  $6.6 \pm 0.4$  years;  $\chi^2_{[1,93]} = 0.21$ ,  $P = 0.65$ , Mann–Whitney *U* test) and among years ( $\chi^2_{[2,92]} = 1.06$ ,  $P = 0.59$ , Mann–Whitney *U* test).

Our final models explained 57% of the variance in calf mass ( $F_{[5,91]} = 24.23$ ,  $P < 0.0001$ ), 34% in calf size ( $F_{[3,93]} = 16.31$ ,  $P < 0.0001$ ), and 20% in calf KFI ( $F_{[1,94]} = 11.74$ ,  $P < 0.0001$ ) at weaning (Table 2). RG calves were heavier ( $51.2 \pm 0.9$  kg), had longer hind feet ( $48.8 \pm 0.3$  cm), and more kidney fat ( $14.1\% \pm 1.0\%$ ) than RAF calves ( $41.6 \pm 0.9$  kg,  $47.2 \pm 0.3$  cm,  $10.1\% \pm 1.0\%$ ) (Table 2, Figs. 2a, 2b, 2c, weaning). Similar to calving, mass of females was positively related to mass (slope =  $0.31 \pm 0.07$ ,  $t_{[1,92]} = 4.73$ ,  $P < 0.0001$ ) and hind-foot length (slope =  $0.06 \pm 0.02$ ,  $t_{[1,93]} = 2.69$ ,  $P = 0.009$ ) of calves. We also detected a positive influence of maternal mass on calf kidney fat (slope =  $0.18 \pm 0.08$ ,  $t_{[1,94]} = 2.22$ ,  $P = 0.023$ ) (Table 2, Fig. 2c, weaning). Heavier females produced larger calves, and contrary to calving, the positive relationships were similar for RG and RAF at weaning (nonsignificant interactions between herd and female mass; calf mass:  $F_{[1,92]} = 0.85$ ,  $P = 0.36$ ; calf size:  $F_{[1,93]} = 0.68$ ,  $P = 0.41$ ; calf fat:  $F_{[1,94]} = 0.21$ ,  $P = 0.65$ ) (Figs. 2a, 2b, 2c, weaning).

Similar to calving, male calves were heavier (Fig. 3b) and taller (hind-foot length:  $48.6 \pm 0.3$  cm) than female calves (hind-foot length:  $47.4 \pm 0.3$  cm) (Table 2, Fig. 3b). The effect of sex, however, did not differ between herds for either mass ( $F_{[1,92]} = 0.16$ ,  $P = 0.69$ ) (Fig. 3b) or body size ( $F_{[1,93]} = 0.07$ ,  $P = 0.79$ ). There was no effect of calf sex on kidney fat ( $F_{[1,94]} = 0.84$ ,  $P = 0.36$ ) at weaning.

Differences in calf mass between herds were larger at weaning than at calving (herd  $\times$  season interaction:  $F_{[3,196]} = 52.77$ ,  $P < 0.0001$ ). The difference between herds corresponded to 8% of body mass at calving (about 0.7 kg, overall mean of  $5.7 \pm 0.1$  kg) and 20% at weaning (about 10 kg, overall mean of  $46.3 \pm 0.8$  kg). The positive effect of female mass on calf mass was also stronger at weaning than at calving (comparison of slopes on standardized data: RG:  $Z = 5.5$ ,  $P < 0.0001$ ; RAF:  $Z = 12.1$ ,  $P < 0.0001$ ) (Fig. 2).

## Discussion

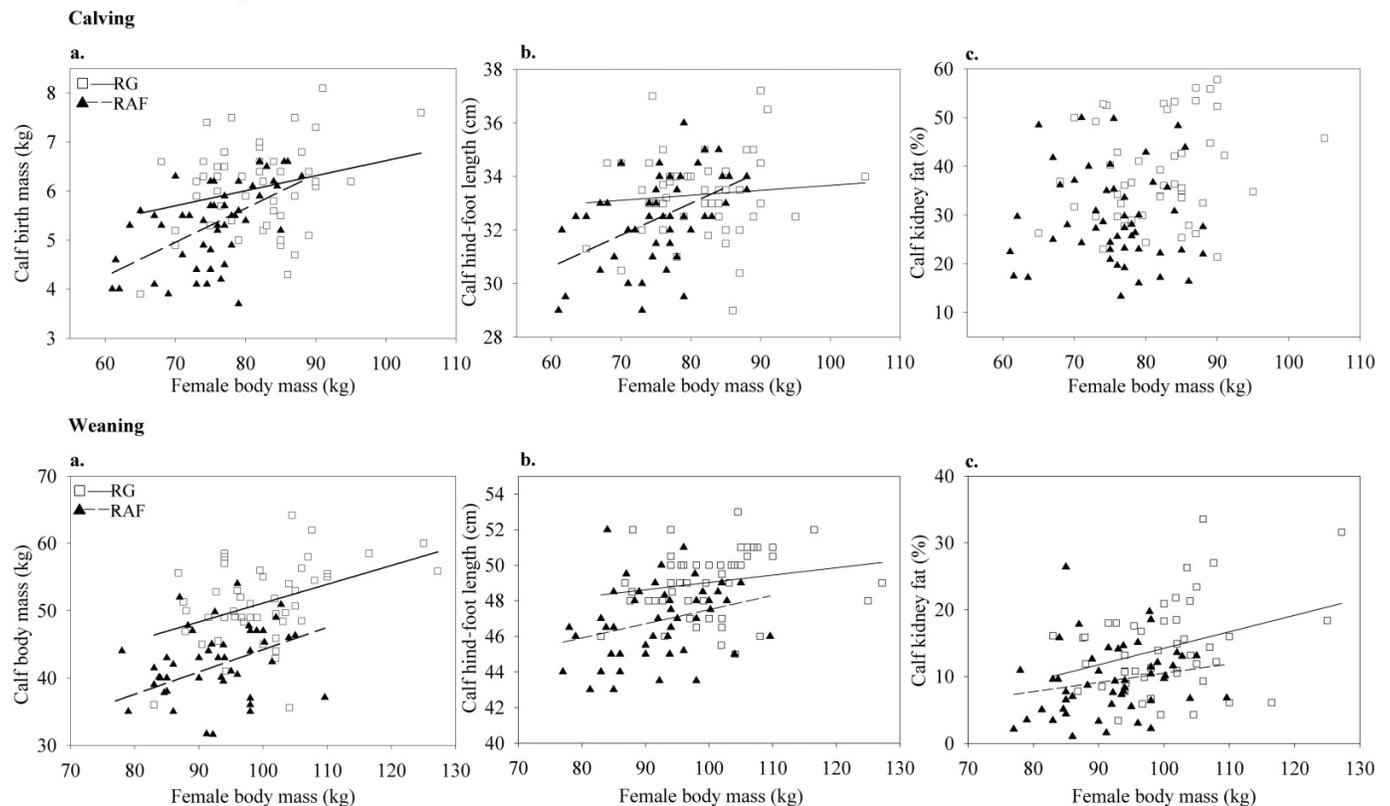
We sought to quantify how population size and maternal traits affected body condition of migratory caribou calves at birth and weaning. We contrasted female–calf pairs of the RG herd, which has recently declined to low population size, with pairs of the much larger RAF herd. Calves of the RAF herd had lower body mass, body size, and kidney fat than calves of the RG herd at both calving and weaning. Differences between herds, however, were much greater at weaning

**Table 2.** Regression models of the effects of year, herd, female mass, sex of calf, and all second-degree interactions on the body mass, size, and fat of migratory caribou calves (*Rangifer tarandus*) at calving and weaning from Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, northern Quebec and Labrador, Canada, 2007–2009.

Season	Calf body condition variable	Effects*	df	F	P
Calving	Body mass (kg); n = 100 pairs	Female body mass	1, 94	24.42	<0.0001
		Calf sex	1, 94	14.68	0.0002
		Herd	1, 94	19.67	<0.0001
	Body size (hind-foot length (cm)); n = 98 pairs	Female body mass × herd	1, 94	3.94	0.046
		Female body mass	1, 94	12.95	0.0005
		Calf sex	1, 94	10.87	0.001
		Herd	1, 94	6.85	0.01
	Body fat (kidney fat (%)); n = 100 pairs	Female body mass × herd	1, 94	6.34	0.014
		Herd	1, 98	26.49	<0.0001
Weaning	Body mass (kg); n = 98 pairs	Female body mass	1, 92	20.71	<0.0001
		Calf sex	1, 92	11.62	0.001
		Herd	1, 92	29.44	<0.0001
		Year	2, 92	6.79	0.002
	Body size (hind-foot length (cm)); n = 97 pairs	Female body mass	1, 93	7.28	0.008
		Calf sex	1, 93	9.38	0.003
		Herd	1, 93	13.61	0.0004
	Body fat (kidney fat (%)); n = 97 pairs	Female body mass	1, 94	5.33	0.023
		Herd	1, 94	7.79	0.006

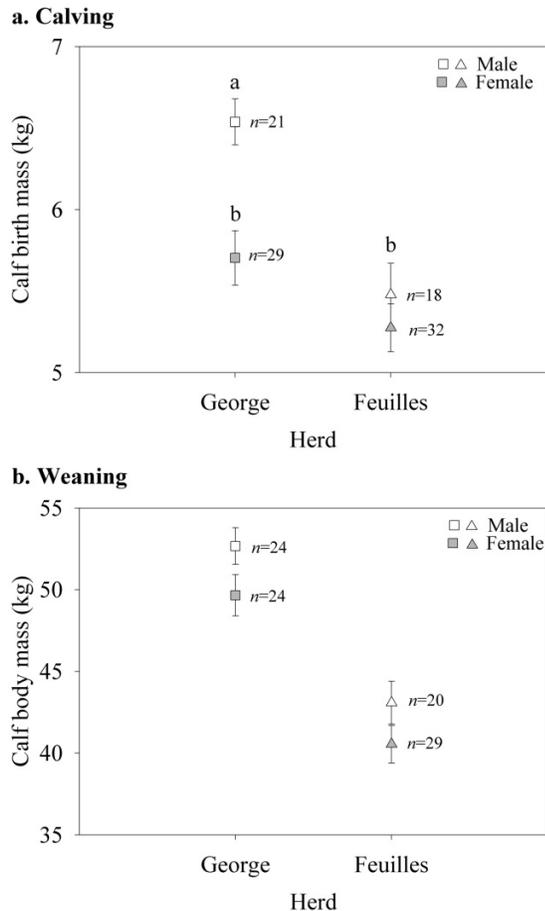
\*Factors and interactions that are not presented were not significant ( $P > 0.05$ ) and were not included in the final model.

**Fig. 2.** Relationships between maternal mass and (a) calf body mass (kg), (b) calf hind-foot length (cm), and (c) calf kidney fat (%) at calving (early June) and at weaning (October–November). Data were collected from 2007 to 2009 on mother–calf pairs of migratory caribou (*Rangifer tarandus*) from Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, northern Quebec and Labrador, Canada. At calving, relationships were not significant with calf hind-foot length for RG and with kidney fat for both herds. At weaning, because there was no significant interaction between maternal mass and herd for calf hind-foot length or kidney fat, only one regression is shown, presenting the relationship with maternal mass for pooled data for both herds.



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**Fig. 3.** (a) Birth mass and (b) weaning mass (mean  $\pm$  SE) of male and female migratory caribou calves (*Rangifer tarandus*) in 2007, 2008, and 2009 from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, northern Quebec and Labrador, Canada. Data were pooled because there were no significant year effects. Means with the same letter do not differ significantly ( $\alpha = 0.05$ ).



than calving, suggesting that summer-range conditions affected calf growth. Although we did not measure calf body condition at both low and high density in each population, the difference in population density among herds likely accounted for some of this variation because high population size should decrease the quantity of forage available per capita. Our results show that the negative effect of population size on calf body condition can be buffered by maternal mass at calving, and that the positive effect of maternal mass is greater at weaning than at calving.

Impacts of high population density on juvenile body condition, growth, and survival are common in mammals (Lindström 1999; Kjellander et al. 2006; Bonenfant et al. 2009). We found that caribou calves were 8% heavier at birth and 20% heavier at weaning in a herd of low population size compared with one with high population size. These results suggest that impact of population size may differ depending on season, because of different energetic demands faced by mothers and offspring. At birth, offspring condition is likely related to maternal condition (Wilson and Festa-Bianchet 2009). For northern ungulates, most fetal growth occurs when maternal body reserves are at their yearly minimum (Schwartz and Hundertmark 1993) and the quality and abun-

dance of forage are low (Weixelman et al. 1998). Body condition of gestating females could impact the allocation of resources to the fetus, particularly in the last trimester of pregnancy when fetal growth rate peaks (Pekins et al. 1998; Chan-McLeod et al. 1999). In our study, females of the RAF were about  $5.8 \pm 0.4$  kg lighter than RG females at calving (Taillon et al. 2011). Lower female body condition resulting in lower offspring birth mass has been related to deep snow in some northern ungulates (Adams 2005). In white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), Mech et al. (1991) showed that winter snow depth reduced birth mass and early survival of fawns. In our study, snow conditions could have affected locomotion during spring migration (Couturier et al. 2010), which coincides with the last trimester of pregnancy. Females of the RAF herd undergo longer spring migrations than the RG herd ( $630 \pm 15$  km vs.  $280 \pm 20$  km, respectively; J. Taillon, M. Festa-Bianchet, and S.D. Côté, unpublished data), which may involve higher energy expenses and lower birth masses. Poor forage on the winter range may also reduce female body condition and fetal development, resulting in early calf death (Roffe 1993) or lower birth mass (Skogland 1984). Few data are available, however, to compare winter-range quality of the RG and RAF herds. Other studies on ungulates also suggest that previous summer range condition and fall nutrition are the principal factors influencing female body condition during gestation (Couturier et al. 2009), conception rates (Simard et al. 2008), and birth masses (Kjellander et al. 2006).

Interestingly, newborns of the RG were heavier and fatter than calves of the RAF. Because the ability of newborns to tolerate energy deficits depends on body stores deposited in utero (Barboza et al. 2009), high kidney fat at birth could improve early survival. Accordingly, newborns of the RG could be better prepared to face harsh climatic conditions compared with newborns of the RAF. The similarity in hind-foot length between herds at calving could be explained by the higher priority for growth of the skeleton compared with other tissues (Klein 1964). Therefore, hind-foot length may not be as sensitive as mass or body fat to a reduction in resources (Toïgo et al. 2006).

Differences in body condition of calves between herds were stronger at weaning than calving. Juvenile body condition at weaning should integrate the direct and indirect effects of weather and density on growth (Forchhammer et al. 2001; Bonenfant et al. 2009). Growth of calves, therefore, depends on the quantity and quality of both forage and milk. Spring climatic conditions, usually related to the timing of the onset of vegetation growth, and summer-range conditions, mostly in terms of forage abundance and quality, are crucial limiting factors for many large herbivores (Clutton-Brock et al. 1997; Griffith et al. 2002; Herfindal et al. 2006). In moose (*Alces alces* (L., 1758)), Sæther and Heim (1993) showed a positive relationship between herb biomass on a female's summer home range and the mass of her calf at the onset of winter. A previous study on migratory caribou of the RG and RAF herds showed that June normalized difference vegetation index (NDVI), a proxy of vegetation greenness (Tucker et al. 2005), positively influenced calf mass in late summer (Couturier et al. 2009). At high population size, increased competition on the summer range can, moreover, influence foraging and nursing behaviours (Therrien et al. 2007) and reduce the

quantity or quality of milk produced by females (Landete-Castillejos et al. 2005). The increasing difference in mass of calves between herds, from 8% at calving to 20% at weaning, suggests a combined effect of direct competition for resources and long-term degradation of the summer habitat. Our results are unlikely to be due to permanent differences among herds, because at the end of the 1980s, when the RG herd was at its peak population size and the RAF herd was still increasing, the opposite trend was evident: RAF calves were about 5 kg heavier than RG calves in late July (Crête and Huot 1993; Couturier et al. 2009).

Small differences in birth mass and fat may reduce early survival (Keech et al. 2000). In caribou, birth mass has been positively related to fall population productivity and proposed as an indicator of changes in population abundance (Couturier et al. 2009). In temperate ungulates, juvenile mass at the onset of winter is thought to be a crucial determinant of survival to 1 year (Gaillard et al. 1997; Hewison et al. 2002; Taillon et al. 2006). Loison et al. (1999), for example, showed that a change of 5 kg in winter body mass corresponded to a 10% variation in winter survival in Norwegian red deer (*Cervus elaphus* L., 1758) calves. Low juvenile body condition can also persist to adulthood (Forchhammer et al. 2001; Pettorelli et al. 2002; Gaillard et al. 2003), reduce reproductive success (Forchhammer et al. 2001), and delay age at first reproduction (Festa-Bianchet et al. 1995; Langvatn et al. 1996).

Consistent with other studies (Côté and Festa-Bianchet 2001; Stopher et al. 2008), we did not detect an effect of maternal age on calf body condition. In both herds, however, some 2.5-year-old females gave birth or weaned calves, providing evidence of possible early primiparity even at high population size. Our data showed that the ability of a female to produce a large calf depended on her own body mass, as reported for other ungulates (Landete-Castillejos et al. 2005; Stopher et al. 2008). In addition, however, we also found that the negative effect of high population size on calf body condition was modulated by maternal traits. At calving, heavy females of the RAF herd (high population size) could produce calves of similar mass as those born in the RG herd (low population size). Light females may be more sensitive to high population size and allocate less to offspring (Stopher et al. 2008), while heavy females may experience no trade-off at high or low population size, as reported in bighorn sheep (*Ovis canadensis* Shaw, 1804) (Festa-Bianchet et al. 1998).

At weaning, the positive relationship between maternal and calf mass was similar between herds. Contrary to calving, heavier females of the RAF did not wean calves as heavy as those weaned by females of the RG herd so that for a female of the same mass, calves weaned in the RG were about 10 kg heavier than those in the RAF. Lactation is the most expensive stage of reproduction and may compromise growth or future reproduction of young females (Ofstedal 1985; Hamel et al. 2009b). At high population size, females could have adopted a conservative strategy and prioritize their own body reserves over lactation (Chan-McLeod et al. 1999). This strategy, referred to as the "selfish cow" (Russell et al. 1993), states that mature females under harsh conditions should favor self-maintenance and future reproduction over offspring growth (Parker et al. 2009). Alternatively, at high population

size, good maternal condition may not be enough to compensate for either low offspring birth mass (Loison et al. 1999) or poor summer forage. In roe deer (*Capreolus capreolus* L., 1758), Hewison et al. (2002) concluded that at high density, there was no possible compensation for low birth mass or poor postnatal growth, leading to lower weaning mass. In red deer, low summer forage availability or quality may increase the costs of lactation and reduce female mass in the fall (Landete-Castillejos et al. 2003) or the deposition of fat reserves before estrus (Clutton-Brock et al. 1997; Clutton-Brock and Coulson 2002).

As reported for other polygynous ungulates (Loison et al. 1999; Kjellander et al. 2006), male caribou calves were consistently heavier than females. There was no relationship, however, between maternal body condition and calf sex. Sexual mass dimorphism and the effect of population size persisted from calving to weaning. In male ungulates, adult mass increases reproductive success (Mainguy and Côté 2008). Consequently, males born at high density should have lower reproductive success when competing with those born at low density, as shown for Soay sheep (*Ovis aries* L., 1758) (Coltman et al. 1999). For female calves, being born at high density may reduce survival (Forchhammer et al. 2001) and lifetime reproductive success (Kruuk et al. 1999) compared with females born at low population density. According to the potential consequences of a low body mass for either male or female calves, we could expect long-term cohort effects in the RAF herd, which was at high population size during our study.

## Conclusion

The novelty of our study resides in (i) contrasting two periods of the reproductive cycle with different energetic costs for mothers and trade-offs for calves (survival and growth) and (ii) quantifying the influence of both herd size and maternal traits on different aspects of calf body condition: mass, body size, and body fat. Although our data provide direct information on body condition, we still need to assess how forage quality in the late winter and summer ranges affects the body condition of mothers and calves.

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