

## VARIATION IN CALF BODY MASS IN MIGRATORY CARIBOU: THE ROLE OF HABITAT, CLIMATE, AND MOVEMENTS

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Individual differences in body mass exert a major influence on several life-history traits of mammals. We investigated the factors influencing variation in body mass of calves of migratory caribou (*Rangifer tarandus*) at birth (June, 19 years of data) and in autumn (October, 15 years of data) in the Rivière-aux-Feuilles (Feuilles, 1991–2003) herd and the Rivière-George (George, 1978–2003) herd in Québec and Labrador, Canada. Mass at birth (hereafter, birth mass) did not differ between herds, possibly because part of their winter ranges overlapped. However, Feuilles calves were smaller in autumn than George calves, possibly reflecting differences in summer ranges. The birth mass of calves also varied with year, likely as the outcome of both intrinsic and extrinsic factors. Birth and autumn body mass were influenced positively by habitat quality in June, estimated by the normalized difference vegetation index. The North Atlantic Oscillation of the previous winter was positively correlated with autumn mass of the George calves. Previous winter snowfall was negatively related to the mass of George calves, and daily movement rates in summer were negatively correlated with the mass of calves of both herds in autumn. Birth mass was positively related with productivity in October in the George herd and also with productivity 3 and 4 years later, which corresponds to the beginning of reproduction of females. We suggest that a mechanism of delayed quality effect of the calves could have been involved in the decrease of fall productivity and population size of the George herd.

Key words: body mass, caribou, migration, normalized difference vegetation index (NDVI), North Atlantic Oscillation (NAO), *Rangifer tarandus*, snow

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Individual differences in body mass exert a major influence on several life-history traits of mammals (Calder 1996). Among ungulates, larger individuals may experience a higher survival rate (Festa-Bianchet et al. 1997), greater longevity (Bérubé et al. 1999), and hence a higher reproductive success (Festa-Bianchet et al. 1998; Sand 1996) than smaller individuals. Smaller juveniles may have a delayed primiparity (Adams and Dale 1998; Sand 1996) and may give birth to smaller offspring (Steinheim et al. 2002), with negative implications on survival

and reproduction that can last up to adulthood (Festa-Bianchet et al. 2000; Steinheim et al. 2002). Indeed, it has been shown that condition early in life can have long-term consequences for the cohort's life history (Gaillard et al. 2003; Solberg et al. 2004). For newborns that survived the early critical stages of life, a delayed long-term effect of cohort variation may still generate between-cohort differences in phenotypic or genetic quality, or both, and, thereby, in future fitness components (Gaillard et al. 2003). Therefore, it appears critical to understand patterns and causes of variation in juvenile body mass.

Climate (weather) can act on herbivore body mass by modifying energy expenditures associated with thermoregulation (Gotaas et al. 2000), insect harassment (Helle and Kojola 1994; Weladji et al. 2003), movements (Gotaas et al. 2000), or foraging behavior (Fancy and White 1985a). Climate also can

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influence the abundance of forage (Boelman et al. 2005), its quality (Jonasson et al. 1986), and its availability (Barrette and Vandal 1986). In addition to local climate effects (Putman et al. 1996; Weladji et al. 2002), ecological effects of large-scale climatic modes such as the North Atlantic Oscillation (NAO—Hurrell 1995) have recently been described (Forchhammer and Post 2004; Weladji et al. 2002). For example, Weladji and Holand (2003) have shown that an increasing NAO index was negatively correlated with body mass of calves in reindeer (*Rangifer tarandus*) and that increasing population density accentuated the influence of NAO on mass.

In the Québec–Labrador Peninsula in Canada, examination of historical (Elton 1942; Low 1896) and dendroecological data (Boudreau et al. 2003; Payette et al. 2004) suggests that migratory caribou (*R. tarandus*) herds have experienced 2 and possibly 3 population peaks toward the end of each century since 1770. The Québec–Labrador migratory caribou were scarce at the beginning of the 20th century (Elton 1942), but increased to about 1 million animals in the 1990s (Couturier et al. 1996). Two distinct migratory populations are currently recognized in this region (Boulet et al. 2007; Couturier et al. 2004): the Rivière-George (George River; hereafter, George) herd and the Rivière-aux-Feuilles (Leaf River; hereafter, Feuilles) herd.

Demographic variation in those migratory herds led to major changes in space use, and range expansion occurred with increasing population size (Schmelzer and Otto 2003). Messier et al. (1988) hypothesized that food limitation and greater energy expenditures associated with range expansion could be regulating the George population. The summer habitat of the George herd has been degraded during the 1980s by large numbers of caribou (Couturier et al. 1990; Crête and Huot 1993; Manseau et al. 1996). Recent studies have confirmed past degradation but also revealed signs of vegetation recovery, suggesting that the summer habitat of the George herd might be improving (Boudreau et al. 2003; Théau and Duguay 2004).

Life histories and population dynamics of ungulates are influenced by the combined effects of intrinsic and extrinsic factors (Coulson et al. 2001; Gaillard et al. 2003). Because juvenile body mass may affect future survival and reproduction, our objectives were to investigate variations in body mass of calves at birth (19 years of data) and in autumn (15 years of data) in the Feuilles (1991–2003) and George (1978–2003) caribou herds; and assess the influence of summer habitat productivity, climate (weather), and herd movement rate on calf body mass, as well as to explore the relationship between calf body mass and population productivity. We predicted that body mass of calves would differ between herds, be positively correlated to quality of summer habitat, decrease with increasing severity of local and continental climate, be negatively correlated to the herd movement, and be positively correlated with fall productivity of the herd.

## MATERIALS AND METHODS

We studied 2 migratory caribou herds in the Québec–Labrador Peninsula north of 52°N. Both herds winter in the

boreal forest and migrate northward in spring to spend most of the snow-free season in the tundra.

*Caribou herds.*—In 1956, Banfield and Tener (1958) estimated the George herd at approximately 5,000 caribou. The population began to grow in the 1960s and reached 263,000 caribou in 1976, 390,000 ( $\pm 85,000$ , confidence interval at 90%) in 1980 (Couturier et al. 1990), 644,000 ( $\pm 161,000$ ) in 1984, 682,000 ( $\pm 246,000$ ) in 1988 (Crête et al. 1991), 776,000 ( $\pm 104,000$ ) in 1993 (Couturier et al. 1996), and decreased to 385,000 ( $\pm 108,000$ ) in 2001 (Couturier et al. 2004). Recent population estimates corroborate the decline in relative population size expected by Boudreau et al. (2003) based on analysis of tree-ring scars. Le Hénaff (1976) established the existence of a 2nd migratory herd in northern Québec, the Feuilles herd, which increased from 56,000 in 1975 to 101,000 ( $\pm 43,000$ ) in 1983, 121,000 ( $\pm 56,000$ ) in 1986, 276,000 ( $\pm 76,000$ ) in 1991, and 1,193,000 ( $\pm 565,000$ ) in 2001 (Couturier et al. 2004). Because of the large confidence interval of the 2001 estimate of the size of the Feuilles herd, Couturier et al. (2004) recommended to take the lower confidence limit or 628,000 caribou as a basis for management. Using mortality data from radiotracked animals and productivity data from necropsies (pregnancy rate) as well as ground classification in autumn (calves per 100 females), Crête et al. (1996) studied the demographic trends of the George herd from 1984 to 1992. They reported an annual finite rate of increase of 1.05 on average between 1984 and 1989, and 0.94 for the years 1990–1992. Dendroecological (Boudreau et al. 2003) and lichen abundance (Boudreau and Payette 2004a, 2004b) studies also suggested that the George herd increased in the 1970s and 1980s, but declined in the early 1990s. Based on these results and considering the large confidence intervals of the 1988 and 1993 population surveys, we speculated that the George herd was increasing until 1989, but started to decrease after that. The Feuilles herd was rapidly increasing during the entire study period (see also Payette et al. 2004).

Seasonal ranges of the 2 migratory herds are well known from an extensive radiotracking monitoring program that began in the late 1970s (Boulet et al. 2007; Couturier et al. 2004). Most adult females (93.4%) are philopatric to their respective calving grounds, which are separated by  $>800$  km (Boulet et al. 2007). Historical information suggests that these calving grounds have been used since the end of the 19th century (Low 1896). There is no overlap of summer ranges between the 2 herds although partial range overlap (about one-third) can occur from October to early spring based on many aerial surveys, as well as locations from very-high-frequency and satellite radiotracking (Couturier et al. 2004; S. Couturier, pers. obs.). Satellite radiotracking has shown that rutting range overlap (near 23 October) was 10% on average (range 0–35%) between 1994 and 2001 (Boulet et al. 2007).

*Caribou data.*—Calves were weighed soon after birth in early June (hereafter, birth mass) and in late October (hereafter, autumn mass). Newborn calves were located during helicopter flights over the calving grounds. Once on the ground, calves were captured on foot after short chases (Adams 2005; Skogland 1984). Sex was determined and birth mass was

recorded to the nearest 0.1 kg using a Pesola spring scale (Pesola AG, Baar, Switzerland). Because older calves can easily outrun a person, newborns caught were considered <3–4 days old. We did not adjust birth mass of calves for small differences in age because it was  $\pm 2$  days at most and calves in captivity do not gain much weight during their first 2 days of life ( $0.02 \text{ kg/day} \pm 0.04 \text{ SE}$ ,  $n = 5$ —S. Couturier, pers. obs.). Handling time was usually <1 min and the mother reunited with her calf shortly thereafter. We weighed calves in the fall during necropsies or live captures. Autumn data were collected mostly (81% of the data) between 9 October and 9 November, and masses were adjusted using linear regression (e.g., Weladji and Holand 2003) to 23 October or 135 days old, assuming that birth occurs on 10 June.

Since 1973 during the rutting season, thousands of caribou have been classified from the ground by sex and age through an extensive radiotracking and survey program (Couturier et al. 2004). In this paper, annual fall productivity of each herd was estimated using the calves per 100 adult females ( $\geq 1.5$  years of age) ratios computed from the classification data. We tested correlations between the means of calf mass and fall productivity of the current year. Delayed quality effects also were tested using correlations between the calf masses and fall productivity delayed by 1–7 years.

Laval University Animal Care Committee approved the study and the capture methods met the principles and guidelines of the Canadian Council on Animal Care. All methods also met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

*Habitat and climate data.*—We used the normalized difference vegetation index (NDVI) to assess summer habitat productivity. This remote-sensing index has been used to describe arctic vegetation (Mynemi et al. 1997; Tømmervik et al. 2004) and is correlated with plant biomass (Boelman et al. 2005). NDVI has been used to assess the influence of habitat on life-history traits of ungulates (Griffith et al. 2002; Pettorelli et al. 2005, 2006, 2007). We used monthly NDVI averages (June–September 1981–2002) of cloud-free images at quarter degrees of latitude and longitude (Tucker et al. 2005; [http://islsdp2.sesda.com/ISLSCP2\\_1/html\\_pages/islsdp2\\_home.html](http://islsdp2.sesda.com/ISLSCP2_1/html_pages/islsdp2_home.html)). Water, snow, and ice can be detected with NDVI and those pixels were excluded from the analyses. The NDVI mean monthly values for each year and herd originated from  $8 \times 8$ -km pixels and were estimated for the George ( $55^\circ\text{--}58^\circ 30'\text{N}$ ,  $62^\circ\text{--}68^\circ\text{W}$ ) and Feuilles ( $58^\circ\text{--}61^\circ 30'\text{N}$ ,  $70^\circ\text{--}77^\circ\text{W}$ ) herd summer ranges. Those areas included calving grounds and were used each year by caribou according to satellite radiotracking data (S. Couturier, pers. obs.). We used weather data from the Meteorological Service of Canada for the Kuujuaq station ( $58^\circ 6'\text{N}$ ,  $68^\circ 25'\text{W}$ ) from 1973 to 2003 to compute the following annual variables: average minimal temperature in winter ( $^\circ\text{C}$ , December–March), snowfall in winter (cm, December–March), and the sum of degree-days ( $\geq 0^\circ\text{C}$ ) for the daily maximal temperature for each month between May and September. We used the winter (December–March) index of the NAO (Hurrell 1995; [www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html](http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html)) to describe continental climate. The NAO

is a large-scale fluctuation in atmospheric mass between the subtropical (centered on the Azores) and the subpolar (centered on Iceland) North Atlantic regions. In our study area, the NAO was negatively correlated with snowfall ( $r = -0.53$ ,  $P = 0.002$ ) and minimum winter temperature ( $r = -0.42$ ,  $P = 0.019$ ).

*Movements.*—Adult female caribou ( $\geq 1.5$  years) were captured with a net gun from a helicopter or with a boat during water-crossing. Females were fitted with satellite radiocollars (Argos Inc., Largo, Maryland) and located every 4 or 5 days until their death because collars were continuously replaced every 2 or 3 years. Individuals were monitored for 2.5 years on average (range 1–10 years). For the George herd, the mean number of radiocollared females per year (1986–2003) was 23 (range 5–30), whereas for the Feuilles herd on average 12 females (range 7–14) were monitored annually (1993–2003). Validation of satellite locations was performed (Boudreau et al. 2003; Boulet et al. 2007) and we obtained, after filtering, 21,503 and 7,455 locations for the George and the Feuilles herds, respectively. Individual daily movement rate (km/day) was estimated for each radiocollared female from successive locations ((distance in km/time in hours)  $\times 24$ ). This method underestimates true movements because it supposes linear displacements between successive locations. We used the average daily movement rate for each year and herd as a proxy of the energetic costs (Fancy and White 1985b) related to herd movements. We divided the yearly migration cycle into 2 periods to match our sampling for calf mass. First, we calculated mean daily movement during the summer (hereafter,  $\text{Movement}_{\text{Summer}}$ ) from 10 June (mean birth date) to 23 October to analyze the effect of movement on body mass of calves in autumn. Second, we estimated the mean daily movement for the rest of the year (24 October–9 June) to analyze the relationship between female movement during the previous winter (hereafter,  $\text{Movement}_{\text{Winter}}$ ) and birth mass of calves.

*Statistical analyses.*—A general linear model was fitted on body mass with factors sex, herd, year, and their interactions. Interactions were later removed because none were significant. For each herd, the climate, habitat, and movement covariables also were individually fitted in a general linear mixed model, while accounting for the variable sex. The following covariables were tested separately: herd NDVI in June ( $\text{NDVI}_{\text{June}}$ ),  $\text{Movement}_{\text{Summer}}$ ,  $\text{Movement}_{\text{Winter}}$ , NAO of the previous winter ( $\text{NAO}_{t-1}$ ), snowfall of the previous winter ( $\text{Snow}_{t-1}$ ), average minimum temperature of the previous winter ( $\text{Temp}_{\text{Winter}_{t-1}}$ ), degree-days in July of the year of birth ( $\text{Deg.-days}_{\text{July}}$ ) and of the previous year ( $\text{Deg.-days}_{\text{July}_{t-1}}$ ). Degree-days in July were selected because they are positively related to insect harassment (Couturier et al. 2004; Weladji et al. 2003). Sex, covariables, and their interactions were defined as fixed and year as a random factor in the mixed models. Interactions were later removed because none were significant. Each covariable was tested 1 at a time as in Reimers et al. (2005) to avoid problems related to overparameterization. No measure was repeated on the same calf. Means are presented with their standard error (SE). All analyses were

**TABLE 1.**—Body mass (mean in kg, *SE*, and sample size) at birth and in autumn of migratory caribou (*Rangifer tarandus*) calves from the Rivière-George herd and the Rivière-aux-Feuilles herd, Québec-Labrador Peninsula (Canada), by cohort and by herd. Individual autumn masses were adjusted to 23 October using linear regressions.

Cohort	George herd						Feuilles herd					
	Birth mass			Autumn mass			Birth mass			Autumn mass		
	$\bar{X}$	<i>SE</i>	<i>n</i>	$\bar{X}$	<i>SE</i>	<i>n</i>	$\bar{X}$	<i>SE</i>	<i>n</i>	$\bar{X}$	<i>SE</i>	<i>n</i>
1978 <sup>a</sup>	7.56	0.25	24									
1979 <sup>a</sup>	7.43	0.74	3									
1981 <sup>b</sup>	6.44	0.28	16									
1985 <sup>b</sup>	6.76	0.10	102	33.31	2.01	4						
1986	6.64	0.20	24	41.67	1.63	21						
1987	6.64	0.27	14									
1988	6.25	0.25	18									
1991							6.29	0.19	19			
1992	5.08	0.10	49	45.03	1.01	25						
1993	6.86	0.17	44	45.15	1.93	16	6.80		1			
1994	5.76	0.18	49	46.17	0.87	19	6.56	0.57	7			
1995	5.86	0.18	36	46.26	1.71	24	6.01	0.15	31	43.94	1.15	7
1996	5.05	0.16	35	39.59	1.08	27	5.34	0.16	35	39.10	0.90	23
1997	6.14	0.13	63	44.89	1.22	23	5.46	0.41	9	43.26	1.28	21
1998	5.99	0.19	28	46.42	1.22	20	6.05	0.23	10	47.36	1.03	22
1999	6.05		1				6.37	0.22	17			
2000	5.40	0.31	20	44.30	1.58	27	5.15	0.17	12	37.52	1.01	24
2001	5.94	0.17	21	48.47	1.44	18	5.98	0.23	23	46.34	1.46	9
2002	5.29	0.23	16	44.97	1.46	13	5.31	0.17	27	38.33	1.46	16
2003	6.02	0.15	15				5.77	0.26	17			
Males	6.26	0.07	308	44.88	0.67	120	5.97	0.09	116	43.74	0.85	48
Females	6.00	0.07	270	43.94	0.59	117	5.57	0.10	92	40.39	0.70	74
All	6.14	0.05	578	44.42	0.45	237	5.79	0.07	208	41.70	0.56	122

<sup>a</sup> A. T. Bergerud, unpubl. data.

<sup>b</sup> S. N. Luttich, unpubl. data.

performed with SPSS version 11 for Macintosh OS X (Chicago, Illinois).

## RESULTS

Birth mass of George calves was  $6.77 \pm 0.08$  kg ( $n = 201$ ) from 1978 to 1989 during herd growth (Table 1), but later decreased to  $5.81 \pm 0.06$  kg ( $n = 377$ ) from 1990 to 2003. The body mass of newborns in the Feuilles herd showed a nearly significant decline between 1991 and 2003 during a period of demographic growth ( $r = -0.560$ ,  $P = 0.058$ ). Time series of birth masses were correlated between the 2 herds ( $r = 0.733$ ,  $P = 0.010$ ). The autumn mass of George calves increased between 1985 and 2002 ( $r = 0.670$ ,  $P = 0.017$ ), but this relationship was not significant when 1985 was removed ( $P = 0.203$ ). No time trend was observed in the autumn mass for the Feuilles herd ( $r = -0.202$ ,  $P = 0.663$ ). The correlation between the 2 time series of autumn mass was high but only approached significance ( $r = 0.671$ ,  $P = 0.099$ ). There was no relationship between birth and autumn mass averages in the George herd ( $r = -0.269$ ,  $P = 0.398$ ), although there was a strong correlation between these variables for the Feuilles herd ( $r = 0.926$ ,  $P = 0.003$ ).

*Influence of sex, herd, and year.*—Body mass differed between sexes, with males being heavier than females by  $0.35 \pm 0.09$  kg at birth and  $1.83 \pm 0.75$  kg in autumn (Table 2). Mass did not differ between the herds at birth, but in

autumn George calves were  $2.50 \pm 0.75$  kg heavier than Feuilles calves. Mass varied significantly between years both at birth ( $F = 10.85$ ,  $df = 9, 12$ ,  $P < 0.001$ ) and in autumn ( $F = 9.62$ ,  $df = 6, 21$ ,  $P < 0.001$ ). The cohorts of 1992, 1996, 2000, and 2002 had particularly low masses.

*Temporal variations in climate, habitat, and movements.*—Between 1973 and 2003, snowfall did not show any significant linear time trend, nor did minimal winter temperature or NAO (all  $rs \leq 0.225$ ,  $Ps \geq 0.223$ ). We noted a significant warming trend in May ( $r = 0.381$ ,  $P = 0.034$ ), July ( $r = 0.372$ ,  $P = 0.039$ ), and September ( $r = 0.568$ ,  $P = 0.001$ ), but some spring seasons remained particularly cool (e.g., 1992, 1996, and 2002). From June to September, NDVI annual means were higher for the George herd compared to the Feuilles herd (Fig. 1). NDVI increased in time in June ( $r = 0.457$ ,  $P = 0.037$ ), July ( $r = 0.512$ ,  $P = 0.015$ ), and August ( $r = 0.528$ ,  $P = 0.012$ ) for the Feuilles herd (Fig. 1). No other significant temporal trends for NDVI were found (all  $rs \leq 0.262$ ,  $Ps \geq 0.239$ ; Fig. 1). NDVI of both herds for each month between June and August were correlated with degree-days for the same month ( $rs \geq 0.434$ ,  $Ps \leq 0.044$ , except for George herd in July). Degree-days in May also were correlated with NDVI in June for both herds ( $rs \geq 0.652$ ,  $Ps \leq 0.001$ ). Movement<sub>Summer</sub> ( $r = -0.743$ ,  $P \leq 0.001$ ) and Movement<sub>Winter</sub> ( $r = -0.794$ ,  $P \leq 0.001$ ) decreased for the George herd between 1986 and 2003 (Fig. 2). Movement was high at the end of the demo-

graphic growth period, and later decreased during a population decline. Movement<sub>Summer</sub> increased ( $r = 0.634, P = 0.036$ ), but Movement<sub>Winter</sub> did not change ( $r = 0.352, P = 0.319$ ) for the Feuilles herd between 1993 and 2003 (Fig. 2). From 1993 to 2003, Movement<sub>Summer</sub> was significantly higher ( $t = -6.68, d.f. = 5,406, P < 0.001$ ) for the Feuilles ( $10.72 \pm 0.15$  km/day) than for the George herd ( $9.56 \pm 0.09$  km/day). During the same period, Movement<sub>Winter</sub> was also significantly higher ( $t = -8.75, d.f. = 7,787, P < 0.001$ ) for the Feuilles ( $7.66 \pm 0.11$  km/day) than for the George herd ( $6.47 \pm 0.15$  km/day).

*Influence of habitat, movement, and climate.*—For the George herd, birth mass was related to NDVI<sub>June</sub>, Snow<sub>t-1</sub>, and Deg.-days<sub>July<sub>t-1</sub></sub>, whereas autumn mass was related with NDVI<sub>June</sub>, Movement<sub>Summer</sub>, NAO<sub>t-1</sub>, and Snow<sub>t-1</sub> (Table 3a). For each 0.1 increment of NDVI<sub>June</sub>, the calves were 0.53 kg heavier at birth and 1.67 kg heavier in autumn. When Snow<sub>t-1</sub> increased by 10 cm, calves were 0.07 kg lighter at birth and 0.30 kg lighter in autumn. Birth mass decreased by 0.09 kg for each increase of 10 Deg.-days<sub>July<sub>t-1</sub></sub>. Autumn mass decreased by 0.16 kg for each increase of 0.1 km/day in summer movements and increased by 0.48 kg for each increase of 1 NAO<sub>t-1</sub> unit.

None of the variables significantly explained variation in birth mass of Feuilles calves, but NDVI<sub>June</sub> approached significance ( $P = 0.064$ ; Table 3b). In autumn, the model with NDVI<sub>June</sub> was significant with an increase of 6.14 kg in calf mass for each 0.1 unit increase in NDVI. Movement<sub>Summer</sub> also was significantly related to autumn mass, with calves being 0.42 kg lighter on average for each increase of 0.1 km/day of the mean summer movement rate. Temp.<sub>Winter<sub>t-1</sub></sub> was not related to mass in both herds (Table 3).

TABLE 2.—General linear models on calf body mass (kg) at birth and in autumn (adjusted to 23 October) of migratory caribou (*Rangifer tarandus*) from the Rivière-George herd and the Rivière-aux-Feuilles herd, Québec-Labrador Peninsula (Canada). Factors sex, herd, and year were tested and the reference values were females, Feuilles, and 2002, respectively.

Factors	Birth mass <sup>a</sup>			Autumn mass <sup>b</sup>		
	Estimates	SE	P	Estimates	SE	P
Sex	0.35	0.09	0.000	1.83	0.75	0.015
Herd	-0.05	0.11	0.664	2.50	0.75	0.001
Year			0.000			0.000
1993	1.56	0.23	0.000			
1994	0.55	0.21	0.011			
1995	0.66	0.20	0.001	3.37	1.58	0.034
1996	-0.12	0.20	0.536	-2.08	1.41	0.142
1997	0.80	0.20	0.000	2.81	1.45	0.053
1998	0.71	0.23	0.002	5.44	1.46	0.000
1999	1.02	0.29	0.001			
2000	0.04	0.24	0.862	-0.30	1.41	0.833
2001	0.63	0.22	0.004	5.57	1.63	0.001
2002	0			0		

<sup>a</sup> Period 1993–2002, years of monitoring = 10,  $n = 485$  calves,  $r^2 = 0.197$ .

<sup>b</sup> Period 1995–2002, years of monitoring = 7,  $n = 274$  calves,  $r^2 = 0.244$ .

*Calf body mass and fall productivity.*—The annual average birth mass of George calves from 1978 to 2003 was correlated with herd productivity (Fig. 3a;  $r = 0.701, P = 0.001, n = 18$ ). The relationship was not significant for the birth mass of Feuilles calves ( $r = 0.007, P = 0.986, n = 9$ ), nor for autumn mass in both herds but sample sizes were smaller (George:  $r = -0.100, P = 0.756, n = 12$ ; Feuilles:  $r = 0.040, P = 0.932, n = 7$ ). The annual average birth mass of George calves also

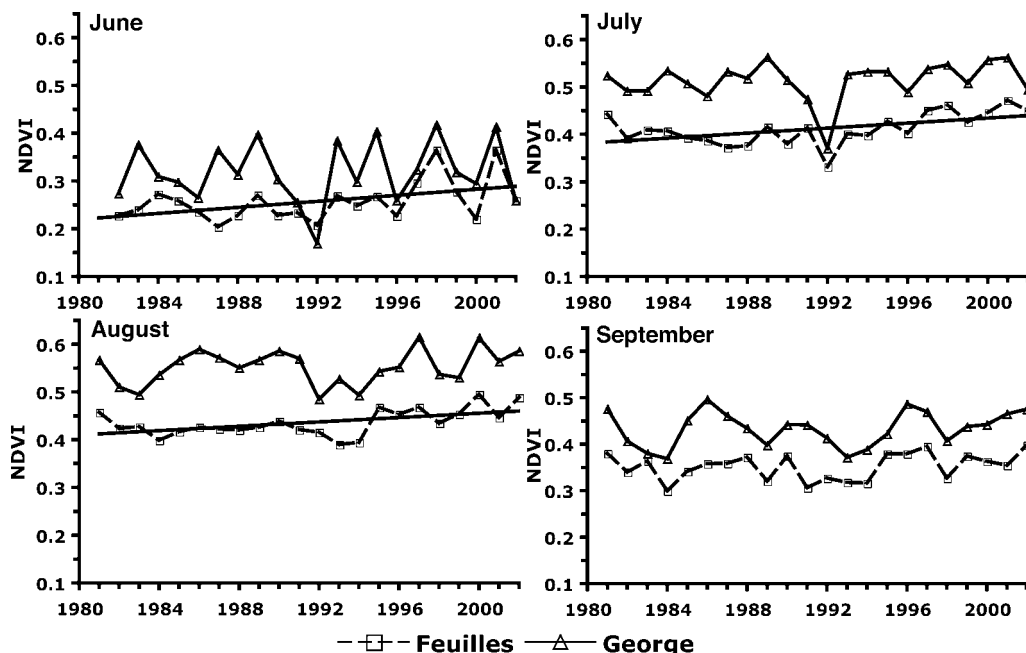


FIG. 1.—Vegetation productivity from 1981 to 2002 estimated by the normalized difference vegetation index (NDVI), which varies from 0 to 1. The monthly averages of summer ranges of the Rivière-George (George) caribou (*Rangifer tarandus*) herd and the Rivière-aux-Feuilles (Feuilles) herd in the Québec-Labrador Peninsula are shown. Regression line is fitted only when significant ( $P \leq 0.05$ ).

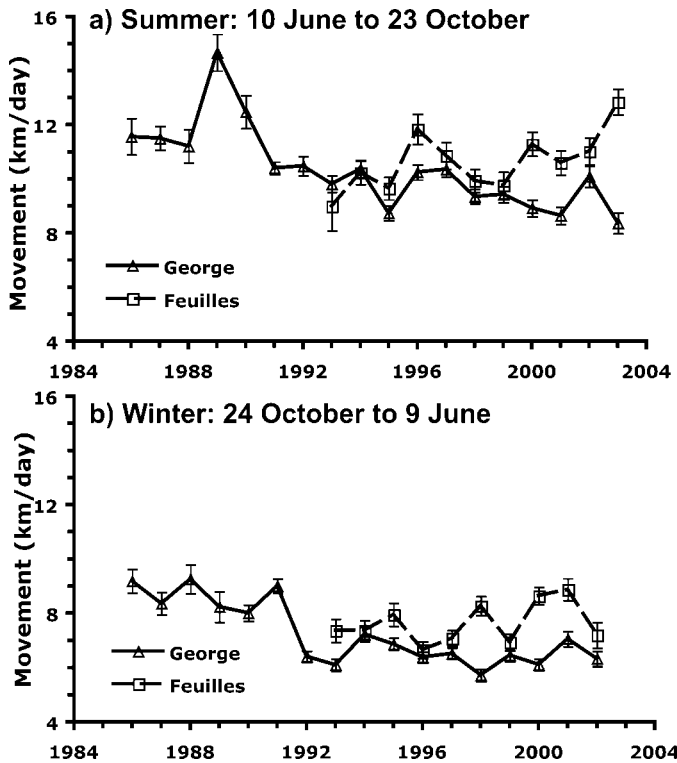


FIG. 2.—Daily movement (means  $\pm$  SE) of adult female caribou (*Rangifer tarandus*) between 1986 and 2003 as estimated by satellite radiotracking for the Rivière-George (George) and the Rivière-aux-Feuilles (Feuilles) herds in the Québec-Labrador Peninsula during a) summer (10 June–23 October), and b) winter (24 October–9 June).

was correlated with herd productivity during fall 3 years later ( $r = 0.577$ ,  $P = 0.024$ ,  $n = 15$ ) and 4 years later ( $r = 0.568$ ,  $P = 0.034$ ,  $n = 14$ ), but not with fall productivity delayed by 1, 2, 5, 6, or 7 years. Fall productivity of the George herd varied on average from 52 calves/100 females during 1973–1983 when the herd was growing, to 37 in 1984–1989 during the last years of herd growth, and to 31 in 1990–2003 when the herd initiated its decline (Fig. 3b), with the lowest values recorded in 2000 (17), 2002 (19), and 1992 (24).

### DISCUSSION

Birth and autumn body masses of caribou calves differed between sexes and years. Time series of body mass were often correlated between herds, suggesting that both herds were affected by common extrinsic factors. In partial agreement with our prediction about herd differences, we found that calves in the George herd were heavier in autumn than those of the Feuilles herd, but that their birth masses did not differ. Results also supported our expectation that habitat productivity during summer would exert a positive influence on body mass at both ages. Only the George herd partly confirmed our prediction that body mass of calves would be lower under conditions of relatively severe winter weather. Body mass of George herd calves was lower with increasing previous-winter snow and temperature in the previous July, and autumn mass increased with increasing NAO index. Also, higher rates of movement nega-

TABLE 3.—Parameter estimates of individual covariables from general linear mixed models on calf body mass (kg) at birth and in autumn for the a) Rivière-George caribou (*Rangifer tarandus*) herd and the b) Rivière-aux-Feuilles herd. Covariables were entered individually in a model with sex and the covariable as fixed effects, and year as a random factor. The subscript  $t-1$  refers to the previous year.

Covariables	Birth mass		Autumn mass	
	Estimates	P	Estimates	P
a) George herd <sup>a</sup>				
NDVI_June	5.31	0.000	16.65	0.020
Movement <sub>Summer</sub>			-1.56	0.014
Movement <sub>Winter</sub>	-0.04	0.743		
NAO <sub>t-1</sub>	0.02	0.723	0.48	0.038
Snow <sub>t-1</sub>	$-6.5 \times 10^{-3}$	0.014	-0.03	0.005
Temp._Winter <sub>t-1</sub>	-0.06	0.339	-0.21	0.498
Deg.-days_July			0.02	0.166
Deg.-days_July <sub>t-1</sub>	$-9.0 \times 10^{-3}$	0.001		
b) Feuilles herd <sup>b</sup>				
NDVI_June	4.70	0.064	61.38	0.000
Movement <sub>Summer</sub>			-4.17	0.001
Movement <sub>Winter</sub>	0.01	0.953		
NAO <sub>t-1</sub>	0.06	0.215	-0.04	0.925
Snow <sub>t-1</sub>	$-6.7 \times 10^{-4}$	0.815	-0.02	0.452
Temp._Winter <sub>t-1</sub>	$-9.8 \times 10^{-3}$	0.884	-0.53	0.475
Deg.-days_July			$1.3 \times 10^{-3}$	0.963
Deg.-days_July <sub>t-1</sub>	$1.9 \times 10^{-4}$	0.962		

<sup>a</sup> Birth: study period = 1987–2002,  $n = 394$  calves; Autumn: study period = 1986–2002,  $n = 233$  calves.

<sup>b</sup> Birth: study period = 1994–2002,  $n = 171$  calves; Autumn: study period = 1995–2002,  $n = 122$  calves.

tively influenced autumn mass in both herds, but not birth mass. Finally, we confirmed that the birth mass of George calves was positively correlated with fall productivity of the herd.

*Influence of sex, herd, and year.*—As expected for sexually dimorphic species, male caribou calves were heavier than females at birth and in autumn as shown in reindeer by Weladji and Holand (2003). George calves were heavier than Feuilles calves in autumn but not at birth, probably because of differences in their summer ranges as compared to winter ranges that they partially share (Schmelzer and Otto 2003; S. Couturier, pers. obs.). In ungulates, birth mass is related to winter nutrition (Skogland 1984), whereas autumn mass is mainly determined by habitat quality in summer (Côté and Festa-Bianchet 2001). The lack of difference between the George and Feuilles herds in birth mass of calves may be only partly explained by overlapping winter ranges, and should be investigated further. Our NDVI results suggest that the summer range of the George herd was of better quality than that of the Feuilles herd (Fig. 1). Accordingly, George calves were heavier in autumn than Feuilles calves during 1995–2002. Valkenburg et al. (2003) also noted that the autumn mass of female calves of the Delta caribou herd in Alaska was higher than that of animals from the Nelchina herd (57.1 versus 52.0 kg), possibly because of better summer nutrition. However, because NDVI is a large-spatial-scale proxy of habitat quality, our study design

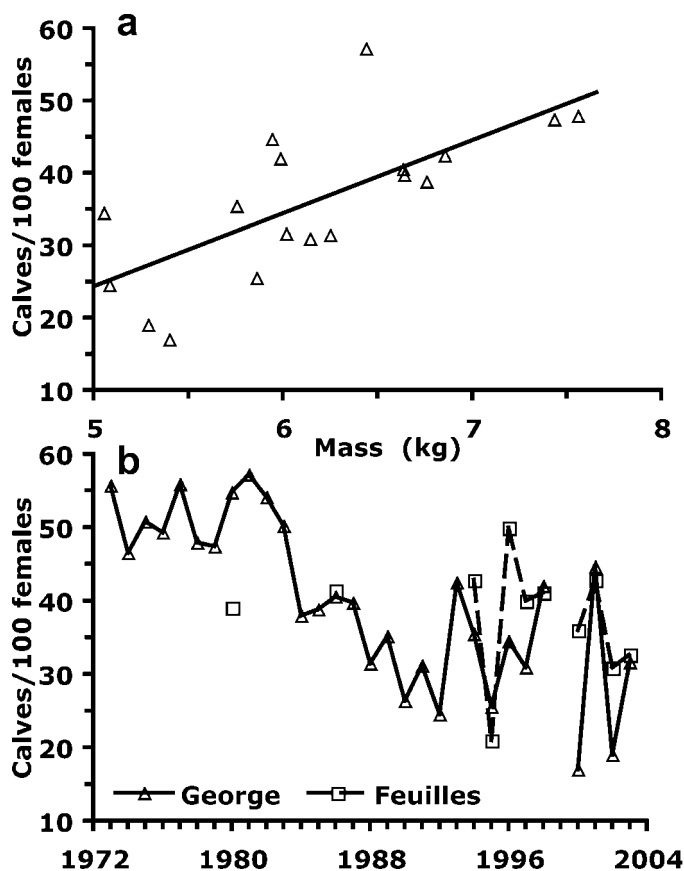


FIG. 3.—Fall productivity relationships for caribou (*Rangifer tarandus*) herds in the Québec–Labrador Peninsula. a) For the Rivière-George herd, regression between fall productivity (calves/100 females) and birth mass (see SE in Table 1) in previous June ( $r = 0.701$ ,  $P = 0.001$ ,  $n = 18$  years), and b) annual fall productivity of the Rivière-George and Rivière-aux-Feuilles herds between 1973 and 2003.

does not capture the possibility that caribou may be able to exploit fine-scale variation in habitat quality and thereby improve their energy balance in areas of apparent poor habitat based on NDVI. Nevertheless, during summers and falls of 2001 and 2002, lactating females of the George herd also were in better condition than those of the Feuilles herd, suggesting that the summer habitat of the George herd was better (Couturier 2007).

Body mass varied among years, and cohorts with small average body mass were often linked to unfavorable climatic events such as snow (Table 3). For example, snowfall in 1995–1996 was the highest of the 1973–2003 period (220 cm compared to a mean of  $132 \pm 7$  cm), and George females gave birth to the smallest calves recorded in the study in spring 1996. This negative influence lasted until October 1996, leading to the 2nd lowest autumn mass observed. Years in which spring conditions were delayed also appeared to have negative impacts, because the mean birth masses of the 1992, 1996, and 2002 cohorts were small and coincided with low degree-days in May and low NDVI in June (Fig. 1). Adams (2005) also showed that severe snow conditions and late springs were associated with low birth mass in caribou.

*Influence of population size.*—Our results suggested that annual variation in calf body mass was mirrored by changes in herd size. Examination of data reported by Drolet and Dauphiné (1976) and Parker (1980), along with those in Table 1, suggests that body mass of calves in the George herd was high in the late 1970s at the start of a period of demographic growth. Subsequently, calf mass appeared to decrease in the 1980s while the George herd was approaching its population peak. The Feuilles herd seems to have followed the same pattern, as suggested by the decreasing trend in birth mass from 1991 to 2003 during population growth. Thus, calf mass appears to decrease when a population is approaching its peak and the following sections present some possible mechanisms for this hypothesis.

*Influence of summer habitat.*—As previously reported for reindeer (Pettorelli et al. 2005), early appearance of green vegetation in spring as indicated by high NDVI in June exerted a positive influence on caribou calf mass. Our research indicated that NDVI in June influenced calf body mass in both herds, confirming the key role of summer range conditions for migratory caribou (Griffith et al. 2002; Manseau et al. 1996).

During winter, caribou subsist primarily on lichens that are low in protein (Parker et al. 2005), so that pregnant females rely heavily on their own body protein reserves to nourish their growing fetus. The increasing costs of late gestation between March and June may lead to tissue catabolism among pregnant females (Chan-McLeod et al. 1999). Poor nutrition in winter reduces birth masses (Skogland 1984) and females with low body and dietary protein will likely give birth to small calves (Chan 1991). However, new vegetation becomes available in the last month of pregnancy (late May–early June), which provides pregnant females access to high-protein food. Having access to this high-quality forage while still pregnant may be crucial for females and influence the mass of their newborns. We used monthly NDVI but recent studies on a shorter time resolution suggested that the timing and rate of changes in primary production during 1st appearance of green vegetation in spring are key indicators of forage quality (Griffith et al. 2002; Pettoelli et al. 2006, 2007). Moreover, the rate of vegetation growth between birth and 3 weeks postpartum is critical to early survival of caribou calves (Griffith et al. 2002).

*Influence of movement.*—Messier et al. (1988) proposed that forage limitation in summer was the predominant regulation mechanism for the George herd, although they added that the increase in energy costs associated with range expansion during population growth also may have a regulatory effect per se. We showed that movement rate in summer was negatively related to autumn mass in both herds. The higher movement for the Feuilles herd in summer likely increased energy costs and could partly explain the lower body mass in autumn for the Feuilles calves compared to George calves. To disentangle habitat and movement effects, we used NDVI data that showed a trend for increasing habitat quality for the Feuilles herd summer range during the period when calf birth mass decreased (Fig. 1), suggesting negative impacts of movement on body mass of calves. We propose that variation in both summer habitat quality (Couturier et al. 1990; Crête and Huot 1993; this

study) and movements play an important role in the regulation of the George herd, likely through effects on the body mass of calves and fall productivity (Fig. 3). Future research should investigate the influence of movement on body condition with a focus on identifying mechanisms driving interannual variation in movements.

*Influence of climate.*—Snowfall the previous winter had a significant negative impact on calf mass at birth and in autumn for the George herd, whereas no significant effect was found for the Feuilles herd, most likely because of a smaller sample size. The negative influence of snow on calf mass also was observed elsewhere in *Rangifer* (Adams 2005; Helle and Kojola 1994; Kumpula and Nieminen 1992) and in other ungulates (Hjeljord and Histøl 1999; Mech et al. 1987). Caribou must dig food craters in winter (Barrette and Vandal 1986) and less snow likely results in energy savings (Fancy and White 1985a, 1985b). However, it is also possible that the negative impact of snow was not related to winter conditions per se but might be indirectly caused by a late snow melt delaying plant growth (Adams and Dale 1998). Pettorelli et al. (2005) found that the influence of winter conditions was weaker than the positive impact of an early start of the growth of vegetation on the mass of reindeer calves.

The NAO was correlated with autumn mass of George calves, but not with that of Feuilles calves. NAO likely acted through reduced snowfall because winter temperature was not related to calf mass (Table 3). The positive NAO phase after the early 1990s translated into colder temperature and less snow in winter in the Québec–Labrador Peninsula (Forchhammer and Post 2004). Other studies have reported NAO effects on body condition or life-history traits of ungulates. For example, Weladji and Holand (2003) have shown in Norway that increasing NAO index had a negative influence on the body mass and growth rate of reindeer calves, whereas the NAO was strongly positively correlated with both winter precipitation ( $r = 0.82$ ,  $P = 0.01$ ) and winter temperature ( $r = 0.83$ ,  $P = 0.01$ ). In contrast, Reimers et al. (2005) did not find any relationship between NAO and body mass of reindeer, but local climate and NAO were weakly correlated in their study ( $r_s \leq 0.282$ ).

Other studies have reported a negative relationship between current summer temperature and calf body mass in autumn (Helle and Kojola 1994; Kumpula and Nieminen 1992; Weladji et al. 2003), which we did not find. Instead, we noted that temperature in July of the previous year was negatively correlated with birth mass of calves. This relationship with temperature could be linked to insect harassment, a key climate-related factor influencing the ecology of caribou (Weladji et al. 2002). It could occur through the negative impact of insects on the condition of females during the previous summer, which may delay ovulation date and decrease the birth mass of calves (Couturier et al. 1990; Skogland 1984). An alternative hypothesis is that high temperatures in July result in lower nutrient quality in plants (Jonasson et al. 1986). The joint influence of poor-quality forage and insect harassment may therefore act as double jeopardy for *Rangifer* (Weladji et al. 2003).

*Calf body mass and fall productivity.*—Survival of young ungulates is positively related to body mass (Adams et al. 1995; Côté and Festa-Bianchet 2001; Festa-Bianchet et al. 1997). We found that mean birth mass of caribou in the George herd was positively related to productivity in the next fall. From Crête et al. (1996) and assuming an adult survival rate of 0.87 (1983–1992 mean), we estimated that fall productivity must be 34 calves/100 females for the George herd to be stable. Despite the complexity of the data sets, we speculate that birth mass (means of both sexes) must be about 6.0 kg for fall productivity to approach 34 calves/100 females (Fig. 3a). This might suggest that when birth mass is lower than 6.0 kg, the George herd should decrease (fall productivity < 34 calves/100 females). However, these productivity ratios must be interpreted with caution because we do not know whether the age distribution of the George herd varied during the study.

Fall productivity was not correlated with mean autumn mass in both herds, suggesting that summer survival was more related to conditions during the previous winter than conditions during the present summer. Birth masses were not different between herds, thus suggesting that protein reserves of females (Parker et al. 2005) were similar, likely because of overlapping fall and winter ranges. Fall productivity of both herds was quite similar (Fig. 3), but pregnancy rates were different at 75% and 52% in 2001–2002 for the George and the Feuilles herds, respectively (Couturier 2007). These results suggest that calves start their lives in similar condition but they encounter contrasting conditions during their 1st summer, which may generate the 2.5-kg difference in autumn masses. The higher autumn mass of calves in the George herd may be partly explained by higher NDVI (Fig. 1), reduced movements in summer (Fig. 2), or selective mortality of small calves in the George herd during summer. Thus, that George herd calves were larger in autumn than Feuilles herd calves does not necessarily imply better range quality or reduced movements, because small calves might have died.

Females appear selfish in the summer and seem to set a priority on replenishing their protein reserves over lactation (Chan-McLeod et al. 1999). Thus, if a young calf is not gaining enough mass in the first 2 months of life, the mother will likely wean it early, leading to its death (Russell and White 2000). In caribou and many other species of ungulates, the body reserves of lactating females in autumn are lower than those of females that are free of the burden of lactation (Chan-McLeod et al. 1999; Gerhart et al. 1997; Simard et al. 2008; S. Couturier, pers. obs.). For nonlactating females, this would result in higher late-winter body reserves, higher birth mass of calves, and presumably better calf survival in summer compared to lactating females under the same winter range conditions. Variations in fall productivity (Fig. 3) might reflect these relationships between protein reserves of females, lactation, and future calf mass and survival.

Cohort effects may have a long-lasting influence, because animals born in difficult years may remain of low quality until adulthood and experience low reproductive success (Festa-Bianchet et al. 2000; Sand 1996; Steinheim et al. 2002). Average birth mass correlated positively with fall productivity

3 and 4 years later in the George herd, indicating that good cohorts with higher birth mass had greater reproductive success 3 and 4 years later. This correlation supports the delayed-quality-effect hypothesis (Gaillard et al. 2003) because 3 or 4 years corresponds to the age of 1st reproduction for females in this population (Crête et al. 1996). The lowest fall productivity for the George herd occurred in 2000 and the smallest cohort of calves born in 1996 was then 4 years old. We hypothesize that this delayed-quality effect was involved in the decline of the George herd and may possibly be acting soon on the demography of the Feuilles herd.

Body mass of juveniles is more sensitive than body mass of adults to environmental and demographic variations (Vincent et al. 1995), and may be a useful parameter for monitoring the general health status of migratory caribou populations (e.g., Morellet et al. 2007). Our results suggest that monitoring body mass of caribou calves at birth and in autumn in combination with surveys of fall productivity could provide managers with a practical measure of winter and summer nutrition, which in turn would provide important insight into the demographic trajectory of migratory caribou. In Alaska, for example, body mass of calves has been used to monitor demographic trajectories in caribou populations (Valkenburg et al. 2003). Our results suggest that monitoring the body mass of calves may help predict when populations are approaching demographic peaks. This information would be useful between population surveys, allowing more timely decisions regarding harvest effort, thereby minimizing the risk of overuse of forage like that seen on the George herd summer habitat in the 1980s.

## RÉSUMÉ

Les différences dans la masse corporelle des individus exercent une influence majeure sur plusieurs traits de l'histoire de vie des mammifères. Chez le caribou migrateur (*Rangifer tarandus*), nous avons étudié les facteurs influençant les variations de la masse corporelle des faons à la naissance (juin, 19 années de données) et à l'automne (octobre, 15 années de données) des troupeaux de la Rivière-aux-Feuilles (Feuilles, 1991–2003) et de la Rivière-George (George, 1978–2003) dans la Péninsule du Québec–Labrador, Canada. La masse à la naissance ne différait pas entre les deux troupeaux en raison probablement du chevauchement partiel de leurs aires hivernales. Toutefois, les faons du Feuilles étaient plus petits à l'automne que ceux du George ce qui reflétait probablement les différences observées entre leurs aires estivales. La masse à la naissance des faons variait également selon l'année à la suite d'une conséquence probable des effets de facteurs intrinsèques et extrinsèques. Les masses à la naissance et à l'automne étaient influencées positivement par la qualité de l'habitat en juin estimée par le normalized difference vegetation index. Le North Atlantic Oscillation de l'hiver précédent était positivement corrélé avec la masse à l'automne des faons du George. Les précipitations de neige de l'hiver précédent étaient négativement corrélées avec la masse des faons du George, tandis que le taux de mouvement journalier en été était négativement corrélé avec la masse des faons à l'automne chez

les deux troupeaux. Dans le troupeau George, la masse à la naissance était positivement corrélée avec la productivité du troupeau en octobre mais également avec la productivité décalée de 3 et 4 ans ce qui correspond au début de la reproduction des femelles. Nous suggérons qu'un mécanisme d'effet retardé de la qualité des faons a été impliqué dans la diminution de la productivité automnale et de la taille de la population du troupeau George.

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