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Reproduction, Growth and Body Composition of Rivière George Caribou in Captivity

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ABSTRACT. Twenty females from the Rivière George caribou herd were captured in April 1987 in northern Quebec and were held in a zoo in Quebec City. Until November 1989, they were kept in an enclosure with a male from the same herd and they were fed *ad libitum* with pelleted concentrates and hay, supplemented with fresh deciduous leaves in summer. Daily food consumption exhibited an annual cycle, peaking at over 100 $g \cdot kg^{-0.75}$ in summer and decreasing to *ca.* 70 $g \cdot kg^{-0.75}$ by late winter. Food consumption decreased at the end of the last summer, due perhaps to lower hay quality. Mean body mass of adult females increased from 90 kg upon arrival at the zoo to ≈ 115 kg in the autumn of 1987, ≈ 125 kg in September 1988, and then decreased to 113 kg in November 1989. Pregnancy rate increased from 65% in 1987 to 82% in 1989 for animals captured in the wild. Two females born in captivity in 1987 became pregnant as yearlings, while 1 of 3 yearling females ovulated in 1989. Mass of calves at birth was higher in 1988 and 1989 than in 1987, while the calving period advanced by two weeks in the last two years. Growth of calves in summer was unrelated to birth mass and was higher in 1987 and 1988 (450-490 $g \cdot d^{-1}$) than in 1989 (365 $g \cdot d^{-1}$). Male calves grew at a faster rate than females. Carcass composition, in terms of lipids, protein and water, did not differ much between calves and yearlings born in captivity and free-ranging animals collected in 1983-84. However, the mass of each component was much lower in free-ranging lactating females than in captive ones. All captive females that had ovulated before necropsy, including one yearling, had at least 7.2 kg of stored fat.

Key words: captivity, caribou, fat, growth, George River, nutrition, protein, Quebec, *Rangifer tarandus*, reproduction

RÉSUMÉ. Vingt femelles du troupeau de caribous de la rivière George furent capturées en avril 1987 dans le nord du Québec et amenées à un *jardin zoologique* à Québec. En compagnie d'un mâle du même troupeau, elles furent nourries à volonté de moulée et de foin, additionnés de feuilles d'arbustes décidus en été, jusqu'en novembre 1989. La consommation journalière de nourriture suivit un cycle annuel, culminant en été à plus de 100 $g \cdot kg^{-0.75}$, et diminuant autour de 70 $g \cdot kg^{-0.75}$ à la fin de l'hiver. La prise alimentaire diminua à la fin du dernier été, vraisemblablement à cause de la qualité amoindrie du foin. La masse corporelle des femelles adultes augmenta de 90 kg à leur arrivée au zoo, à ≈ 115 kg à l'automne 1987, à ≈ 125 kg à l'automne 1988, pour redescendre à 113 kg en novembre 1989. Le taux de gestation des animaux capturés en nature augmenta de 65% en 1987 à 82% en 1989. Les deux femelles nées en captivité en 1987 furent fécondées à l'âge d'un an et demi, alors qu'une un-an sur trois ovula en 1989. La masse des faons à la naissance fut plus grande en 1988 et 1989 qu'en 1987, et les naissances furent devancées de deux semaines au cours des deux dernières années. La croissance des faons durant leur premier été n'était pas reliée à leur masse à la naissance et elle fut plus rapide en 1987 et 1988 (450-490 $g \cdot j^{-1}$) qu'en 1989 (365 $g \cdot j^{-1}$). Les faons mâles crûrent à un rythme plus rapide que les femelles. La composition des carcasses, en termes de lipides, de protéines et d'eau ne différait pas beaucoup entre les faons et les un-an nés en captivité et des animaux en liberté récoltés en 1983-1984. Par contre la masse de chaque composante était beaucoup plus faible en nature qu'en captivité pour les femelles en lactation. Toutes les femelles captives ayant ovulé avant la nécropsie, incluant une un-an, possédaient au moins 7.2 kg de réserves de lipides.

Mots clés: captivité, caribou, croissance, gras, nutrition, protéine, Québec, *Rangifer tarandus*, reproduction, rivière George

INTRODUCTION

Ecologists have been interested for a long time in assessing the physical condition of large mammals. Marrow and kidney fat were the first indices used to evaluate the body reserves of free-ranging cervids (Cheatum, 1949; Riney, 1955). However, the existence of an annual cycle in body mass of cervids living in a seasonal environment (Mitchell *et al.*, 1976; Leader-Williams and Ricketts, 1982; Kay *et al.*, 1984; Schwartz *et al.*, 1984) complicates the use of such indices (Huot, 1988). Kidney mass itself was shown to vary annually (Dauphiné, 1975; Leader-Williams and Ricketts, 1982; Van Vuren and Coblentz, 1985). Moreover, Verme and Ozoga (1980) found that lipogenesis constituted an obligatory physiological event in autumn, even for white-tailed deer (*Odocoileus virginianus* Zimm.) kept on a low nutritional plane. On the other hand, catabolism of both protein and fat stores was shown to be an adaptation to the low quality of forage available in winter (Leader-Williams and Ricketts, 1982; Reimers *et al.*, 1982). Finally, Skogland (1990) suggested that range quality had an intergeneration effect on body composition of reindeer (*Rangifer tarandus* L.). More recent measurements of carcass composition has led to a better understanding of storage and utilization of body reserves in northern cervids (Huot, 1982; Reimers *et al.*, 1982; Adamczewski *et al.*, 1987; DelGiudice *et al.*, 1990).

In boreal ecosystems, poor physical condition is more common in late winter and can result in increased vulnerability to predation (Potvin and Jolicoeur, 1988), disease (Leader-Williams, 1982), perinatal mortality (Verme, 1977; Skogland, 1983, 1984) and starvation (Barrett, 1982; Gates *et al.*, 1986). Conversely, summer range has been shown to influence growth rate, body size and calving time in Norwegian wild reindeer (Reimers *et al.*, 1983; Skogland, 1983), and growth of immature moose (*Alces alces* L.) in Norway was related to summer precipitation (Saether, 1985).

Body reserves also influence reproduction, but the physiological mechanisms involved remain unknown. Both body mass and fat reserves are related to fertility in reindeer and caribou (Dauphiné, 1976; Leader-Williams and Ricketts, 1982; Thomas, 1982; Reimers, 1983) and in red deer (*Cervus*

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elaphus L.; Albon *et al.*, 1986) but are influenced in turn by age (Albon *et al.*, 1986; Tyler, 1990) and reproductive status (Dauphiné, 1976; Leader-Williams and Ricketts, 1982; Huot, 1988; Tyler, 1990). On the other hand, Tyler (1987) found that pregnant reindeer spare fat in late gestation for lactation.

The Rivière George caribou herd (RGCH) in northern Quebec-Labrador, which peaked at over 600 000 individuals by the mid-eighties (Crête *et al.*, 1989; Hearn *et al.*, 1990), is thought to be regulated by food availability on the summer range (Couturier *et al.*, 1987; Crête *et al.*, 1990). Rivière George females completely exhaust their fat reserves during the first month of lactation, while fat reserves remain stable during the same period for a neighbouring herd inhabiting a good range (M. Crête and J. Huot, unpubl.); growth of calves is also slower on the Rivière George summer range. Differences in carcass composition of lactating and non-lactating Rivière George caribou in autumn indicate that currently females cannot fully recover from lactation before the mating season (Huot, 1988). An increase in the number of non-breeding females probably explains in large part the decreasing number of calves observed in autumn composition counts (Couturier *et al.*, 1990).

The objectives of this study were to describe the growth and the annual fluctuation in body mass of Rivière George caribou fed *ad libitum* and to measure carcass composition of such animals in autumn. In order to minimize the number of sacrificed caribou, we restricted our study to females, with statistically minimal sample size per age class.

METHODS

Between 1 and 10 April 1987, 20 adult (≥3-year-old) female caribou belonging to the RGCH were captured 40 km northwest of Kuujjuaq en route to their calving ground in northern Quebec-Labrador (coordinates: 58°20′;68°45′). They were driven with snowmobiles into nets set between trees (DesMeules *et al.*, 1971), manually restrained, tied and moved on sleighs to a 1000 m^2 holding enclosure in Kuujjuaq (Vandal and Huot, 1989). The enclosure contained terrestrial lichens, in addition to a feeder in which pelleted feed and hay were offered; terrestrial lichens were consumed during the first week, and supplementary food afterward. Animals were flown to the Jardin zoologique du Québec in Quebec City using a DC-3 aircraft on 23 and 29 April. Seven animals succumbed to capture myopathy in the initial weeks following their arrival at the zoo, due to prolonged physical immobilization.

At the zoo, caribou and their offspring were kept in a forested enclosure covering approximately 1500 m^2. The enclosure contained a sheltered scale with two holding paddocks that allowed weighing of animals without chemical or manual immobilization. Forage was offered in three feeders, two for pelleted feed and one for hay; water was available year-round.

Animals received daily pelleted feed (Table 1) and second cut alfalfa-clover hay, both provided *ad libitum*. The quantity of forage provided daily was measured in kilograms for the concentrate and in fractions of a bale for hay. On one occasion, 10 bales were weighed and averaged 17.6 kg (SE=0.8). Most pelleted feed was consumed by caribou, but 10-20% of the hay was spoiled. During the growing season, forage was supplemented daily with bundles of deciduous shrubs; the dry mass of food consumed per bundle, measured on three different occasions during the summer of 1988, averaged 0.780 kg (SE=0.127; n=3). Daily forage consumption was expressed in terms of metabolic body mass (body mass$^{0.75}$). Calves were included in the computation starting on 1 August, considering that calf growth was related to concentrate intake after the age of 45 days (Lavigueur, 1991).

TABLE 1. Composition of pelleted feed provided to captive Rivière George caribou and their offspring, Quebec City, April 1987 - November 1989

Ingredient	Percentage	Digestible energy[a] (kcal·kg)
Ground corn	30.0	4012
Ground wheat	12.5	3880
Ground bran	13.8	3086
Molasses and sugar cane	7.5	4012
Ground beet pulp	10.0	2604
Dehydrated grass flour	10.0	2778
Soybean flour	8.8	3704
Fish powder	5.5	3748
Ground bone	1.0	—
Iodized salt	1.0	—
Overall	100.1	3482

[a] Digestible energy for cattle based on 100% dry matter (Crampton and Harris, 1969).

Caribou were weighed at approximately one-month intervals between August and April; no weighing was performed during late gestation and early lactation to prevent abortion or accident to the offspring when herding the animals into the holding paddocks. Newborns were weighed at birth and irregularly until August, when they were handled with the adults.

A 2½-year-old male originating from the RGCH but born at the zoo was introduced in the enclosure in October 1987 and kept with the captive herd until September 1989. In addition, one male born from a captive female in 1987 was kept in the enclosure until March 1989; he was observed mating with some females in the fall of 1988 (L. Lavigueur, pers. comm. 1989). Other males born in captivity were removed from the enclosure during their first winter of life.

The animals were observed very closely at the time of parturition and during lactation (Lavigueur, 1991), so that the reproductive history of each individual was known. Calves were weighed at birth (except for two wet stillbirths), sexed, ear-tagged and had their umbilicus disinfected with standard iodine solution. All animals received annual vaccinations against infectious bovine rhinotracheitis (IBR), bovine viral diarrhoea (BVD) and parainfluenza virus (PI_3) (Triangle 3, Laboratoires Ayerst, Saint-Laurent, Quebec H4R 1J6) and a polyvalent vaccine against clostridial infections (Tasvax 8, Coopers Agropharm Inc., Ajax, Ontario L1S 3C5). Regular faecal exones were conducted and during periodic weighing animals received injections of Ivomec (Ivomec, MSD Agnet, Pointe Claire, Quebec H9R 4P8) to control internal and external parasites.

At the end of the experiment on 21 November 1989, all females born in captivity plus four lactating animals born in the wild were killed after being live-weighed. All other animals had been removed from the enclosure one month earlier. Body length was measured with a tape from the tip of the nose to the last caudal vertebra, and hind foot length was measured from the tip of the hoof to the tip of the calcaneum. Mandible length was measured according to Bergerud (1964).

Carcass composition was estimated in terms of fat, protein, water and ash. Ash content is very stable throughout the year in caribou (Huot, 1989) and was assumed constant at 4.4% of the ingesta-free body mass (IFBM). Percent fat of IFBM was predicted with the equation (J. Huot, unpubl.): % fat = 0.091 KFFI - 1.382 (R^2 = 0.92), where KFFI is the kidney femur fat index; it is similar to Connolly's (1981) CONDINDEX, without subtracting 20 from the kidney fat index in order to eliminate negative values. Protein of IFBM was derived from the multiple regression (J. Huot, unpubl.): Protein (kg) = 0.0747 PERO + 1.68 AGE + 2.11 (R^2 = 0.93), where PERO is the wet mass (g) of the peroneus muscle and AGE equals 0 for calves and 1 for other animals. Water content of IFBM was estimated with the equation (J. Huot, unpubl.): Water (kg) = 0.247 WPERO + 6.25 AGE + 8.92 (R^2 = 0.92), where WPERO is the water content (g) of the peroneus and AGE is defined as in the preceding equation. WPERO was estimated as 73.9% (SE=0.2; n=65) of PERO. IFBM was obtained by summing masses of fat, protein, water and ash.

At the autopsy, the uterus and ovaries were removed, fixed with formaldehyde and preserved in alcohol. The ovaries were cut in 1-2 mm slices and examined macroscopically for corpora lutea. The first incisors of the adults were removed for age determination through counts of cementum annuli (Ouellet, 1977).

The analysis of variance served to evaluate the effect of year and sex on calf mass at birth and on their growth rate during their first summer of life. In this last case, the slope of the linear regression relating the age of each calf in days up to 120-140 days and their mass served as the dependent variable; moreover the analysis of variance was weighted by the inverse of the variance of the slope. The interaction year X sex was not significant in both analyses ($P>0.05$) and it was removed from the final model. The analysis of variance was also used to test the effect of month and reproductive status of adult females on their body mass; the analysis was performed for each year separately. The procedures REG and GLM of SAS (SAS Institute Inc., 1985) were used for the statistical analysis; the LSMEANS statement served to compute weighted growth rate of calves according to the year of birth and sex of the animal. Date of calving was compared between years with the Kolmogorov-Smirnov test (Siegel, 1956).

RESULTS

Caribou increased their food consumption rapidly after their arrival at the zoo (Fig. 1). Thereafter, daily intake exhibited an annual cycle, peaking at over 100 g·kg$^{-0.75}$ body mass in mid-summer and reaching a minimum of *ca.* 70 g·kg$^{-0.75}$ by late winter; the figures include spoiled hay. Food consumption was lower at the end of summer 1989 than during the two preceding ones. Concentrate made up the bulk of daily rations, averaging 17% protein content and providing 3482 kcal·kg^{-1} of digestible energy. Protein content of hay was tested in 1987 only and ranged between 14.5 and 15.5%; its digestible energy can be estimated at 2212 kcal·kg^{-1} (Crampton and Harris, 1969).

At the time of arrival the mass of female caribou averaged 90 kg, and it did not differ ($P>0.5$) between surviving individuals and those that died from myopathy. Adult body mass reached ≈115 kg the following autumn. It attained a maximum in the autumn of 1988 at ≈125 kg (Fig. 2). Adult body mass varied significantly by month in all three years (1987, $P<0.001$; 1988, $P<0.001$; 1989, $P=0.057$) but by reproductive status in 1989 only ($P=0.021$); in 1988, the interaction between month and reproductive status was significant ($P<0.001$). Most of this variation was attributable to the fact that body mass of pregnant females remained stable in mid-gestation while non-pregnant adults tended to decrease in size.

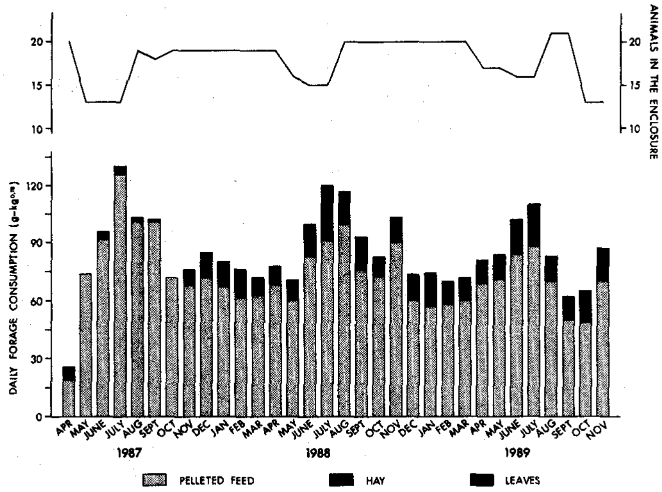

FIG. 1. Average daily food consumption of captive Rivière George caribou kept at the Jardin zoologique du Québec, April 1987 - November 1989.

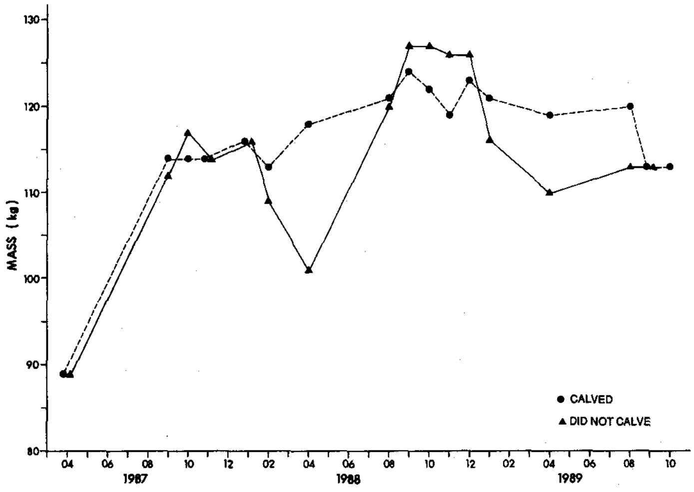

FIG. 2. Live body mass fluctuation in captive female Rivière George caribou according to their reproductive status in the current year, Quebec City, April 1987 - November 1989.

Thirteen of the 20 females brought to the zoo were pregnant (Table 2). Pregnancy rate increased progressively to reach 82% in 1989 among original females; in addition, the two animals born in captivity in June 1987 bred as yearlings and calved in 1989. One or two pregnancies resulted in stillbirth each spring, while one female died after delivery in 1988 and 1989. The survival of calves born alive varied between 63 and 75% during the experiment. Necropsy suggested that mortality was due to septicemia (3), weakness-inanition (2), trauma (1), nephrosis (1) and unknown cause (1). At birth, calves weighed less in 1987 than during the following two springs ($P=0.03$), but body mass did not differ significantly between sexes ($P=0.22$). Calving occurred about two weeks later in 1987 than in 1988 and 1989 and covered a longer period in 1988 (Fig. 3). Calving time did not differ statistically ($P>0.05$) between years according to the Kolmogorov-Smirnov test, mostly due to small sample size.

Calf growth during their first four months of life averaged 450 g·d⁻¹ in 1987 and 488 g in 1988, but no significant difference was found between the two years (Table 3). However, growth was significantly ($P<0.005$) lower in the last summer, averaging 365 g·d⁻¹. Overall, male calves gained body mass at a faster rate than females by 65 g·d⁻¹.

TABLE 2. Reproduction of Rivière George caribou kept in captivity in Quebec City, April 1987 - November 1989

	1987	1988	1989
Pregnancy rate (%)	65 (20[a])	75 (12)	82[d] (11)
Stillbirth (%)	11 (9)	11 (9)	27 (11)
Survival of calves born alive (%)	75 (8)	63 (8)	63 (8)
Female mortality at calving (%)	0 (13)	13 (8)	9 (11)
Birth mass of calves[b] (kg)			
males	6.4 (0.4; 6)[c]	7.8 (1.3; 4)	9.6 (0.2; 2)
females	5.5 (0.3; 2)	8.1 (0.7; 4)	7.2 (0.5; 6)

[a] Sample size; all animals ≥34 months old at their arrival at the zoo in April 1987.
[b] Including animals that died soon after birth.
[c] S.E.; n.
[d] In addition two 2-year-olds born in captivity were pregnant in 1989.

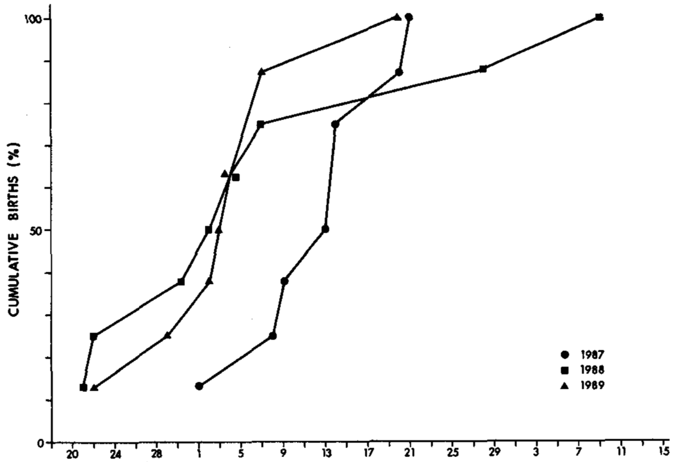

FIG. 3. Chronology of calf births in captive Rivière George caribou, Quebec City, 1987-89. One stillbirth born in September 1989 is not included.

Growth was not related to body mass at birth ($R^2=0.002$; $P=0.88$) or to mother live mass in the preceding mating season ($R^2=0.10$; $P=0.24$).

Calf growth ceased for a few months during their first winter of life, to resume the following spring (Fig. 4). Two females born in 1987 did not increase their body mass between the age of 18 and 30 months, the period during which they were pregnant and nursed a calf. The only male born in captivity that was kept more than one year reached 136 kg when it was removed from the enclosure at the age of 22 months.

At necropsy, body mass of yearlings and 2-year-old animals was similar, but almost 20 kg lower than that of adults (Table 4). Mandibular and hind foot lengths were also greater

TABLE 3. Mean growth rate of Rivière George caribou calves born in captivity during their first four months of life according to the year and sex, Quebec City (growth rates were estimated with linear regression and were weighted with the LSMEANS statement [SAS Institute Inc., 1985])

	Growth rate (g·d⁻¹)	S.E.	n	Different from (P<0.005)
Year				
1987	450	18	6	1989
1988	488	13	5	1989
1989	365	13	5	1987-88
Sex				
Male	469	13	10	Female
Female	400	12	8	Male

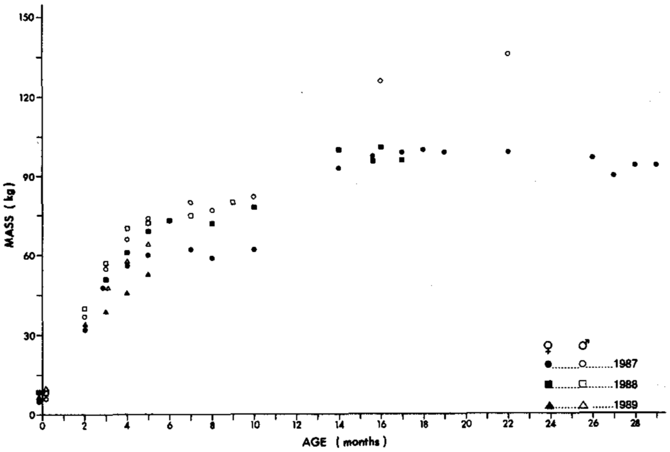

FIG. 4. Growth of Rivière George caribou born in captivity in Quebec City, 1987-89.

TABLE 4. Some morphological characteristics (mean [SE]) of Rivière George caribou and their offspring in November 1989 after 2.5 years of captivity in Quebec City (all animals were females)

	Live mass (kg)	Total length (cm)	Mandible length (cm)	Hind foot length (cm)
Calf (3[a])	53 (3)	140.7 (2.3)	20.9 (0.2)	49.0 (0.6)
Yearling (3)	96 (3)	179.7 (7.0)	28.3 (0.2)	53.7 (0.3)
2½ years old (2)	94 (9)	183.5 (1.5)	28.6 (0.6)	53.0 (2.0)
Adult (4)	113 (1)	176.3 (6.2)	29.5 (0.2)	56.5 (0.6)

[a] Sample size.

in adult females, but total body length, though variable, averaged the same in yearlings, 2-year-olds and adults. Age of adults varied between 6½ and 8½ years.

Estimated IFBM (Table 5) averaged 76% of total body mass in calves, yearling and adults and 82% for the 2-year-olds. Mass of adult carcass fat was almost triple that of calves, while mass of protein was double. Protein content was uniform among all age classes at 23%, but fat content increased with age. IFBM water content varied inversely with that of fat. Ovulation occurred in 1 yearling, 1 2-year-old and 3 adults, but one ovary was lost at autopsy for 1 yearling and 1 2-year-old. Mass of fat reserves constituted the most striking difference when comparing animals that ovulated with those that did not (Table 5). Corpora lutea was present in all animals having more than 7.2 kg (7.8%) of lipids, regardless of age. The yearling and the adult that did not ovulate accumulated 4.5 kg, or 5.3% and 6.5% of fat respectively. The 2-year-old female that lost her calf soon after birth had 8.6 kg (11.2%) of lipids in fall and ovulated, in comparison to only 3.0 kg (3.9%) for the other animal in the same age group that was still lactating; no corpora lutea were observed in the single ovary recovered from this animal. The same was also true in the case of the yearling female for which only one ovary was collected; this animal had 3.0 kg (4.2%) of stored fat.

DISCUSSION

At the outset of the experiment, we wanted to obtain reference animals to evaluate the physical condition of free-ranging Rivière George caribou. We decided to take animals into captivity and feed them *ad libitum* because a set point appears to exist in caribou (Adamczewski *et al.*, 1987) so that animals do not tend to develop obesity. Although 7 out of the 20 original animals died upon their arrival at the zoo, there is no reason to suspect selection for large animals, as body mass of surviving and deceased caribou did not differ. Feed intake per metabolic unit varied annually within the same bounds as for reindeer (Ryg and Jacobsen, 1982) or moose (Schwartz *et al.*, 1984), but forage consumption decreased at the end of the last summer, which affected calf growth and body mass of older animals. We don't know the reason why consumption diminished, but we suspect that hay quality might have been lower than in the previous summers, which may have reduced the passage rate in the rumen. Calves gained 365 $g \cdot d^{-1}$ on average during the last summer, as compared to 450 and 488 $g \cdot d^{-1}$ during the first and the second summer respectively. In 1988, growth of free-ranging calves in northern Quebec averaged 268 $g \cdot d^{-1}$ for Rivière George caribou, as compared to 377 $g \cdot d^{-1}$ for Rivière aux Feuilles calves (M. Crête and J. Huot, unpubl.), which live on a better range (Crête *et al.*, 1990). We conclude that our animals were in better condition in 1988 than in 1989 and that they corresponded to caribou living on a good, but not exceptional, summer range when they were slaughtered.

Improved nutrition markedly influenced reproduction of our small captive herd. In free-ranging Rivière George caribou at peak density, yearlings ceased to breed while adult pregnancy rate decreased to 76%. Moreover, calving was delayed by two weeks and birth mass averaged less than 7 kg in both sexes (Couturier *et al.*, 1990). In captivity, the two calves born in 1987 reached puberty as yearlings, while one out of three ovulated in 1989. In addition, the male born in captivity was observed to copulate as a yearling in 1988 (L. Lavigueur, pers. obs. 1988), and adult pregnancy rate increased from 65% in 1987 to 82% in 1989. Calving date advanced by two weeks during the last two springs, apparently in response to improved nutrition, to coincide with the calving season observed when the RGCH was expanding (Couturier *et al.*, 1990). The presence of only 1 male in the enclosure with 12 adult females during the 1987 rut may have contributed to prolonging the calving period in 1988. Finally, calf mass at birth increased significantly with *ad libitum* feeding.

Survival of the 29 calves born in captivity was 55% over the three years. This rate is lower than the 69% measured over 15 years in an experimental herd of Finnish reindeer, excluding predation (Eloranta and Nieminen, 1986). This observed survival is much lower than the expected 90-93% for well-managed red deer (Blaxter and Hamilton, 1980). High calf mortality may have been caused by overfeeding with concentrates during late gestation, which seemingly provoked dystocias and apparent lactation failure in captive reindeer and wapiti (Blanchard and Hauer, 1986; Hudson

TABLE 5. Estimated carcass composition of Rivière George caribou and their offspring in November 1989 after 2.5 years of captivity in Quebec City (data are divided according to animal age and occurrence of ovulation in the weeks preceding the autopsy; all animals were females)

	Ingesta-free body mass (kg)	Fat		Protein		Water	
		kg	% IFBM	kg	% IFBM	kg	% IFBM
Calf (3[a])	40 (4[b])	2.8 (0.9[b])	6.6 (1.6[b])	9.3 (0.8[b])	23.1 (2.0[b])	26.4 (2.1[b])	65.8 (1.4[b])
Yearling (3)	73 (4)	5.2 (1.5)	6.9 (1.7)	17.3 (0.6)	23.5 (0.7)	48.1 (1.5)	65.2 (1.3)
2-year-old (2)	77 (<1)	5.8 (2.8)	7.6 (3.7)	17.9 (0.8)	23.3 (1.1)	49.7 (1.9)	64.8 (2.6)
6- to 8-year-old (4)	86 (2)	7.3 (1.1)	8.5 (1.3)	20.1 (0.6)	23.3 (0.4)	55.1 (1.5)	63.8 (0.9)
Ovulation[c] (5)	84 (2)	8.3 (0.4)	10.0 (0.7)	19.1 (0.8)	22.8 (0.3)	52.6 (1.7)	62.8 (0.4)
No ovulation[d] (2)	77 (7)	4.5 (0)	5.9 (0.6)	18.4 (2.0)	23.9 (0.3)	50.7 (5.1)	65.8 (0.3)

[a] Sample size.
[b] S.E.
[c] 1 yearling, 1 2-year-old and 3 6- to 8-year-old.
[d] 1 yearling, 1 6- to 8-year-old.

et al., 1991). Perinatal mortality is equally high for underweight and overweight red deer calves (Fennessy *et al.*, 1990). Calf survival might have been improved by varying concentrate quality according to that of natural forage (Gauthier *et al.*, 1989; Crête *et al.*, 1990), with low protein content in winter (Klein, 1990), as was done with experimental reindeer (Heiskari and Nieminen, 1990). On the other hand, caribou are adapted to being born in a cold environment when germs are less active, and calves of this species may be more susceptible to infection than other cervids born in temperate climates, as is the case for muskoxen (*Ovibos moschatus* Zimm.; Blake *et al.*, 1989). High animal density in the enclosure certainly also increased exposure to infectious agents.

The role of fat reserves in ovulation and successful reproduction is still controversial (Bronson and Manning, 1991). For species such as caribou that spare body reserves for the birth of their progeny (Thomas, 1990), fat reserves at parturition are probably vital for the survival of offsprings. Tyler (1987) showed that reindeer on Svalbard save fat during late gestation for lactation. Lipids exhibit the most pronounced fluctuations of all body components with respect to reproduction in caribou. In an evolutionary perspective, there should be physiological mechanisms in caribou that evaluate the chances of successful reproduction of an individual before triggering ovulation and implantation based on physical condition during the breeding season. As fat accretion continues after the breeding season in free-ranging caribou (M. Crête and J. Huot, unpubl.), other control mechanisms could provoke abortion if body reserves compromise viable reproduction later during pregnancy. Whether fat reserves during oestrus are the ultimate cause of successful reproduction or just an index of appropriate conditions remains debatable. At least for ovulation, it is thought that reproduction is regulated by whole-body energy balance, with fat stores an important component (Bronson and Manning, 1991). In the absence of males, only fat individuals ovulated in our captive herd in 1989, and it was seemingly their second oestrus based on calving dates in the two previous springs. By contrast, most (19/21) free-ranging Rivière George caribou collected in 1983, 1984 and 1989 ovulated (M. Crête and J. Huot, unpubl.), even if many were very lean (Huot, 1989). Three explanations could account for this difference: 1) small sample size, particularly for captive animals; 2) behavioural stimulation of ovulation in the presence of males; 3) influence of the rate of change in forage quality (constant for captive caribou but decreasing in the wild).

For the subspecies *R. t. caribou*, we suggest the existence of a threshold (Thomas, 1990) around 7 kg of fat reserves in late autumn or early winter necessary for successful reproduction. We base this estimate on the fact that all the animals that ovulated in our sample had at least 7.2 kg of fat (or 7.8% IFBM), which is the average measured in pregnant Rivière George caribou in winter (Huot, 1989). In turn, accumulation of fat reserves would be influenced mostly by nutrition, reproductive history and age. Fat reserves averaged 7.3 kg in our well-fed lactating adults, as compared to 3.9 kg in free-ranging Rivière George caribou in 1983-84 (Huot, 1989). Current (Huot, 1989) and previous lactations also negatively affect accumulation of lipids, as exemplified by the huge difference observed between our two 2-year-old animals and by the fact that the adult that did not ovulate in our captive animals was the only one to have successfully raised a young in 1988 and 1989. Finally sub-adults must utilize some of their energy and protein intake to grow in addition to storing fat, while senescence causes a decrease in fertility for old animals (Eloranta and Nieminen, 1986). In addition, lipogenesis constitutes an obligatory physiological event in autumn (Verme and Ozoga, 1980) and under sub-optimal feeding conditions cervids would accumulate fat while reducing musculature and skeletal development. This idea is supported by the fact that the growth pattern of our animals born in captivity suggests that they would attain a longer body size than their mothers (Table 4) and that adult caribou of the Rivière George herd had shorter body and hind foot lengths than those of the Rivière aux Feuilles herd (M. Crête and J. Huot, unpubl.), although both herds are genetically very similar (Roed *et al.*, 1991). In red deer, Albon *et al.* (1986) found that skeletally small individuals were more likely to be fertile than larger individuals under nutritional constraints.

Comparison can be made between our captive caribou with free-ranging counterparts collected in 1983-84 (Huot, 1989), the time when signs of decreasing productivity first appeared. Indeed, the autumn cow:calf ratio fell from 51 to 40 calves per 100 cows between 1983 and 1984 (Couturier *et al.*, 1990). Wild calves and yearlings were then only slightly different from our animals born in captivity, and free-ranging non-lactating adults had body composition similar to that of our captive adults. However wild lactating hinds differed markedly in all aspects from captive adults. We conclude that already in 1983-84, just before the RGCH peaked (Crête *et al.*, 1989; Hearn *et al.*, 1990), lactating females had difficulty rebuilding their body reserves in preparation for the mating season.

Seemingly, the RGCH is regulated by availability of digestible protein on the range used during the first month of lactation (Crête *et al.*, 1990), which has operated through decreased calf production (Couturier *et al.*, 1990; Crête and Huot, 1991) and increased adult mortality (Hearn *et al.*, 1990). Under such circumstances, some variables can be monitored to evaluate the physical condition of the herd and the recovery of the range. Growth rate of calves during their first summer of life will reflect foraging conditions during the current year; a daily rate varying between 350 and 400 $g \cdot d^{-1}$ would indicate good nutrition. Birth mass and timing of calving would be more sensitive to foraging conditions in the previous years; average birth mass above 7 kg and peak calving in the first week of June would reflect good physical condition of the mothers. Finally, healthy hinds raising an offspring should resemble our captive animals, with autumn IFBM around 85 kg, of which 7-10 kg would be fat. These guidelines will remain true as long as the quality of the winter range does not change.

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