Body-condition dynamics in a northern ungulate gaining fat in winter

Serge Couturier, Steeve D. Côté, Jean Huot, and Robert D. Otto

Abstract: Individual condition generally depends on density and is partly determined by habitat quality and climate. We studied long-term trends in the condition and productivity of female caribou (*Rangifer tarandus* (L., 1758)) in two large migratory herds in the Quebec–Labrador peninsula (Canada), the George and the Feuilles herds. Females from the George herd were in better summer condition than those from the more abundant Feuilles herd in 2001–2002, while it was the opposite in 1988 when the Feuilles herd was less abundant than the George herd. Summer nutrition followed the same pattern between herds through time. Spring body condition of females in the George herd declined from 1976 to the mid-1980s during early population growth. Fall condition, however, did not change from 1983 to 2002 when caribou numbers first peaked and later declined. Pregnancy rates were inversely related to herd size in both herds. Vegetation quality (NDVI) in June was significantly related to body proteins in the fall. Albeit unusual for a northern ungulate, body fat increased from fall to spring in the George herd. We conclude that a relatively small and highly grazed summer range, as well as density-dependent effects, affected summer nutrition and the need to continue lipogenesis during winter.

Résumé : La condition physique des animaux dépend généralement de la densité de la population et est partiellement déterminée par la qualité de l'habitat et le climat. Nous avons étudié les variations à long terme de la condition corporelle et de la productivité des femelles du caribou (*Rangifer tarandus* (L., 1758)) dans deux grands troupeaux migrateurs de la péninsule du Québec–Labrador, les troupeaux George et Feuilles. Les femelles du troupeau George étaient en meilleure condition estivale que celles du plus grand troupeau Feuilles en 2001–2002, tandis que le contraire s'observait en 1988 alors que le troupeau Feuilles était moins abondant que le troupeau George. La nutrition estivale a suivi le même patron temporel chez les deux troupeaux. La condition printanière des femelles du troupeau George s'est détériorée de 1976 jusqu'au milieu des années 1980 durant la phase initiale de croissance démographique du troupeau. La condition automnale, toutefois, n'a pas varié entre 1983 et 2002 alors que les effectifs atteignaient d'abord un sommet, puis déclinaient. Le taux de gestation était inversement relié aux effectifs chez les deux troupeaux. L'abondance de la végétation (NDVI) en juin était significativement reliée aux protéines corporelles en automne. Quoique cela semble inhabituel pour un ongulé nordique, le gras corporel a augmenté entre l'automne et le printemps dans le troupeau George. Nous concluons qu'une aire estivale relativement petite et surpâturée ainsi que des effets dépendants de la densité affectent la nutrition estivale et le besoin de poursuivre la lipogénèse en hiver.

Introduction

Body condition of animals mainly depend on environmental and nutritional influences acting alone or through complex interactions. Environmental stochasticity commonly driven by climate variations can determine the condition of animals through direct (e.g., thermoregulation) and indirect (e.g., food abundance and availability) effects. Density-dependent effects on nutrition and condition can act immediately (Gaillard et al. 2000; Zedrosser et al. 2006) or following a time lag (Messier et al. 1988; Yom-Tov et al. 2007). Density dependence and environmental stochasticity may also interact, as adverse climatic effects on condition might be revealed or exacerbated only at high population densities (Sæther 1997; Coulson et al. 2001; Weladji and Holand 2003; Herfindal et al. 2006). Body condition is fundamental to various life-history traits and thus can influence both survival and reproduction (Cameron 1994; Reading and Clarke 1995; Flydal and Reimers 2001). Breeding decisions are often quality- or condition-dependent and selection against weaker individuals can progressively eliminate low-quality phenotypes, generating population-level effects (Tavecchia et al. 2005). From the individual to the population level, the effects of condition translate into population demography through effects on survival and reproduction (Mahoney and Schaefer 2002), particu-

Received 24 July 2008. Accepted 6 March 2009. Published on the NRC Research Press Web site at cjz.nrc.ca on 7 April 2008.

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larly when density is high and close to the habitat carrying capacity (Keyser et al. 2006).

Because winter is often a limiting season in northern environments, more emphasis has been put on the study of winter nutrition of northern herbivores than on summer nutrition. Summer, however, is a critical period for deposition of body reserves that are essential for future survival and reproduction (Stewart et al. 2005; Therrien et al. 2007). In ungulates, inadequate nutrition in summer reduces pregnancy rates by preventing estrus and ovulation (Cook et al. 2001; Stewart et al. 2005), delaying conception (Cook et al. 2001) and calving (Couturier et al. 1990; Flydal and Reimers 2001), and may result in reductions in size and body reserves (Leader-Williams and Ricketts 1982; Crête and Huot 1993; Mahoney and Schaefer 2002; Herfindal et al. 2006). As northern ungulates acquire body reserves and grow during a brief summer of plant growth, variation in summer nutrition should affect body condition more than variation in winter nutrition, when metabolism is reduced (Hjeljord and Histøl 1999; Lesage et al. 2001). Seasonality is crucial in the ecology of northern ungulates. Although an overwinter decline in condition has been reported in many ungulates (Dauphiné 1976; Renecker and Samuel 1991; Cook et al. 2001), the mechanisms involved are still not fully understood. Most large mammals decrease their metabolic rate and voluntary food intake in winter (Rhind et al. 2002; Arnold et al. 2006). In addition, nocturnal hypometabolism is a mechanism of energy conservation that is associated with peripheral cooling and contributes to lower energy expenditures during winter (Arnold et al. 2004, 2006). Tyler et al. (1999) challenged the conventional view that mass loss and the mobilization of tissue reserves in winter necessarily reflects undernutrition and instead proposed that a seasonal decrease in appetite in winter reduces body condition. Food-intake reduction in winter is considered to have evolved as a physiological adaptation to seasonal food shortage, so that the drive to search for food is reduced when supply is limited (Rhind et al. 2002).

Our study addressed the body-condition dynamics of adult females (≥2 years) from two large migratory caribou (*Rangifer tarandus* (L., 1758)) herds of the Quebec–Labrador peninsula, Canada (north of 53°N, ca. 1 000 000 km^2). The Rivière-George herd (George River herd, hereafter George) and the Rivière-aux-Feuilles herd (Leaf River herd, hereafter Feuilles) are not genetically different (Boulet et al. 2007), but they are ecologically distinct and managed as discrete herds (Couturier et al. 2004). These herds have undergone drastic population variations in the last two centuries characterized by prolonged periods of scarcity followed by shorter periods of abundance (Low 1896; Payette et al. 2004). In the 1880s, migratory caribou were abundant but later declined rapidly and remained extremely low until the 1960s when they started to increase again (Bergerud et al. 2008). The two herds totaled about 1 million caribou in the 1990s (Couturier et al. 2004).

Our objective was to investigate the summer and winter nutrition of adult female caribou through the analysis of body-condition indices. We studied the relationships between body condition on the one hand, and herd size, season, climate, vegetation abundance, and herd productivity on the other. We hypothesized that (H_1) body condition should be inversely related to herd size and we thus predicted that the individuals from the less abundant George herd in 2001–2002 should be in better body condition than those of the Feuilles herd. Based on aboriginal traditional knowledge, we also hypothesized that (H_2) body condition could improve from fall to spring, contrary to what has been observed for most temperate and northern ungulates. Because of poor and small summer habitat (Couturier et al. 1988, 1990; Crête et al. 1990; Crête and Huot 1993) and a relatively good and large winter habitat (Schmelzer and Otto 2003), we predicted that the body condition of females from the George herd should increase from fall to spring. Finally, we hypothesized that (H_3) body condition would be determined by vegetation abundance and climatic factors. We predicted that body condition would be positively influenced by vegetation abundance in June, as estimated by the normalized difference vegetation index (NDVI; Pettorelli et al. 2005, 2007), and by mild continental winter climate, as indexed by the North Atlantic Oscillation (NAO; Hurrell 1995). We also predicted that body condition would be negatively affected by insect harassment as estimated by the degree-days in July (Weladji et al. 2003) and by total snowfall of the previous winter. Caribou must dig food craters in winter (Barrette and Vandal 1986), and less snow is likely associated with lower energy expenditures (Fancy and White 1985).

Materials and methods

The seasonal ranges of the George and Feuilles migratory herds are well known from a VHF radio-tracking program started in the late 1970s and an on-going satellite monitoring program that began in 1986 (see Couturier et al. 2004; Boulet et al. 2007). Most adult females (93%) are philopatric to their respective calving grounds that are separated by about 800 km between the two herds (Boulet et al. 2007). There is no overlap of summer ranges between the two herds, although partial range overlap can occur from October to early spring. Satellite radio-tracking has shown that rutting range overlap (near 23 October) was 10%, on average, (range 0%–35%) between 1994 and 2001 (Boulet et al. 2007). Both herds move southward in the fall to spend the winter in the boreal forest. They migrate northward in the spring toward their respective calving grounds and spend most of the snow-free season on the tundra. Although managed as distinct populations, the George and Feuilles herds are not genetically different (Boulet et al. 2007).

Population trajectories

From about 5 000 animals in 1956 (Banfield and Tener 1958), the George herd reached 263 000 caribou in 1976, 390 000 caribou (confidence interval at 90% or CI = 85 000) in 1980 (Couturier et al. 1990), 644 000 caribou (CI = 161 000) in 1984, 682 000 caribou (CI = 246 000) in 1988 (Crête et al. 1991), and 776 000 caribou (CI = 104 000) in 1993 (Couturier et al. 1996). The George herd later declined to 385 000 caribou (CI = 108 000) in 2001 (Couturier et al. 2004). From 56 000 caribou in 1975, the Feuilles herd increased to 101 000 caribou (CI = 43 000) in 1983, 121 000 caribou (CI = 56 000) in 1986, 276 000 caribou (CI = 76 000) in 1991, and to more than 628 000 cari-

Table 1. Date of sampling and number of animals examined (*n*) in the study of body condition of reproductively active (≥2 years) female caribou (*Rangifer tarandus*) in the Rivière-George herd (George) and the Rivière-aux-Feuilles herd (Feuilles), Quebec–Labrador peninsula, Canada.

	George		Feuilles		
Year	Dates	*n*	Dates	*n*	References
Summer					
1988	27 July	11	22 July	8	Crête and Huot 1993
1993	21–23 July	10			Manseau 1996
2001	16–18 August	12	27–31 July	9	This study
2002	2–4 August	15	28–29 July	15	This study
	Total	48		32	
Fall					
1983	19–24 October	15			Huot 1989
1985	12–21 September	30			This study
1986	3–12 November	19			This study
1987	2–4 November	6			This study
2001	23–31 October	14	24–28 October	9	This study
2002	20–24 October	13	29 October – 3 November	15	This study
	Total	97		24	
Spring					
1976	March	21			Drolet and Dauphiné 1976
1980	3–15 April	103[a]			Parker 1980, 1981
1984	14–16 April	13			Huot 1989
1986	14–22 March	12			This study
1987	5–14 April	23			This study
2002	4–14 March	17			This study
	Total	189			

[a]This sample of 103 adult females includes 6 nonpregnant females.

bou in 2001 (lower confidence limit; see Couturier et al. 2004). Both herds expanded their ranges during demographic growth. Because population numbers were not estimated annually, we used linear interpolations to compute a dummy variable to index annual herd size. Using the annual interpolated herd sizes, we considered a herd arbitrarily "high" when it included over 500 000 individuals, and "low" under this level. Based on this rule, the George herd was considered high between 1983 and 1998 inclusively, and low before and after this period. The Feuilles herd was considered low until 1997 and high after 1997. We were therefore conservative and compared only periods of high vs. low abundance.

Caribou body condition

We collected adult females (≥2 years) over the entire herd ranges delimited by telemetry. After locating caribou aggregations, the first adult female seen was shot. Only one animal per group was taken. We thus consider sampling to be representative and unlikely to be biased by age, size, or reproductive status of individuals. Both reproductive and nonreproductive females were collected, but here we restricted our analyses to reproductively active females that were either gravid in spring or lactating in summer or fall. Using the presence–absence of a fetus during spring necropsies or a pregnancy-specific protein B (PSPB) (Houston et al. 1986) assay (R.G. Sasser, University of Idaho, Moscow, Idaho, USA) for live-captured animals, we computed the pregnancy rate of the herd as the ratio of pregnant females divided by the total number of females examined. Animal capture and culling were done in accordance with guidelines from the Canadian Council on Animal Care; Laval University Animal Care and Use Committee approved all procedures.

Caribou were weighed soon after death to obtain total body mass. After evisceration, the carcass mass (including head, skin, and antlers) was noted. The kidney-fat mass (KIDNEY_FAT, mean of two kidneys) refers to the mass of perinephric fat (not including the fat extending beyond the kidney; Dauphiné 1976). The kidney mass (KIDNEY_MASS, mean of two kidneys) was also taken. The whole femur was collected and frozen within 24 h. Later, to estimate the femur marrow fat percentage (FEMUR_FAT), the femur was broken and about 10 g of marrow from the central portion of the bone was extracted and oven-dried at about 50 °C until the mass stabilized (Neiland 1970). No correction for mineral content was applied. The kidney fat index (KFI) was computed as $KFI = (KIDNEY\_FAT \times KIDNEY\_MASS^{-1}) \times 100$ (Huot 1988). The kidney–femur fat index (KFFI) was also estimated as $KFFI = FEMUR\_FAT + KFI$ (Crête et al. 1993). From Crête et al. (1993), the percentage of body fat was estimated as $\text{body fat} = 0.091 \times KFFI - 1.382$. The muscles peroneus tertius with extensor digitorum longus and extensor digit III attached (PERO, in g) were dissected from the right leg and weighed soon after death to estimate body protein mass (kg) (following Crête et al. (1993): $\text{protein mass} = 0.0747 \times PERO + 3.79$). We also recorded the maximum depth of back fat of adult females and the body

Fig. 1. Body condition of lactating female (≥2 years) caribou (*Rangifer tarandus*) in the Rivière-George (George) and the Rivière-aux-Feuilles (Feuilles) caribou herds of the Quebec–Labrador peninsula (Canada) in (I) summer and (II) fall: (A) body and carcass mass (kg); (B) protein mass (kg); (C) percentage of body fat; and (D) protein in dried rumen contents (%). Means and SE are presented.

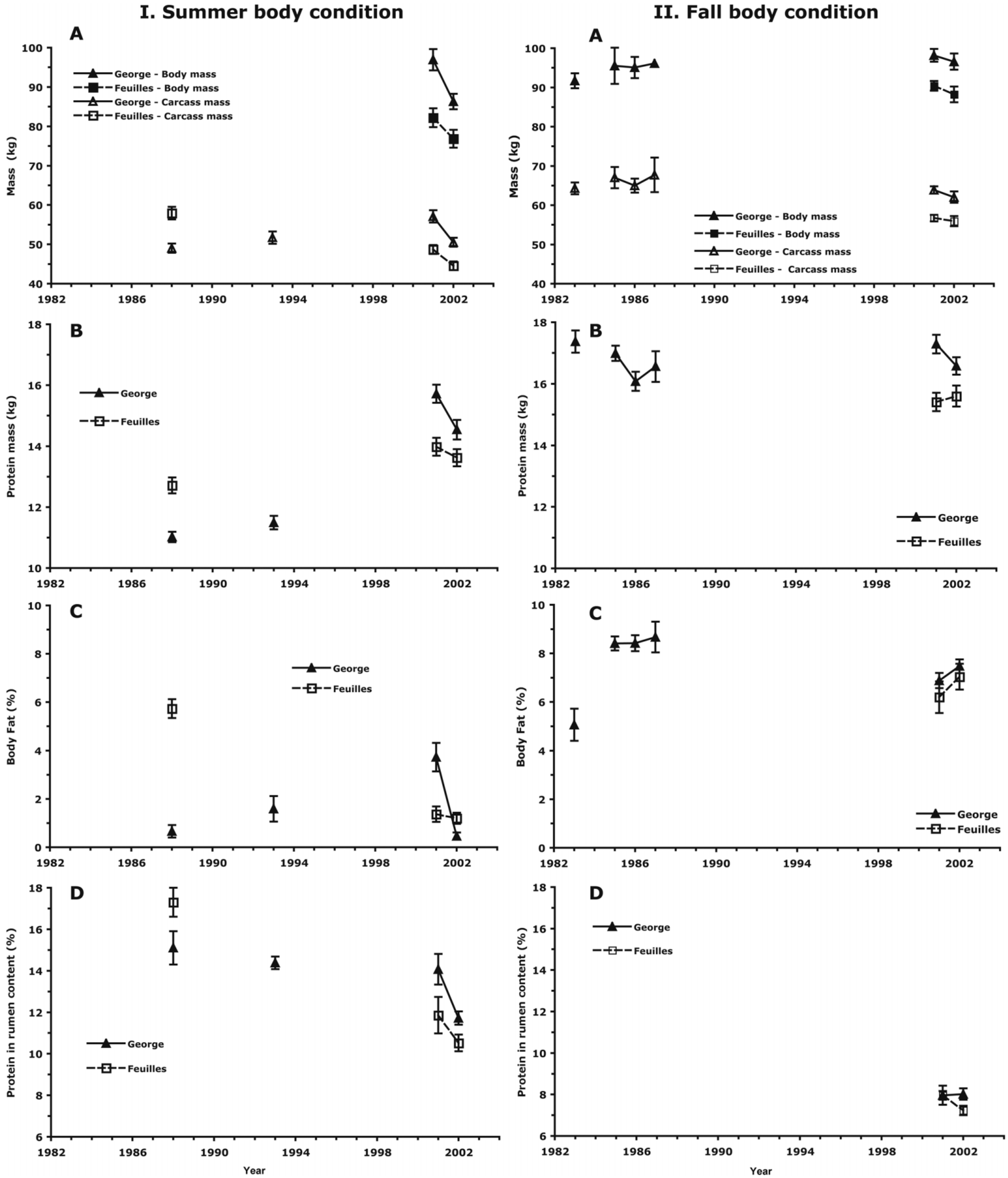


Table 2. Mixed model analyses (year: random factor) of the influence of herd and population size (fixed factor) on the summer body condition of lactating female caribou (*Rangifer tarandus*) from the Rivière-George and the Rivière-aux-Feuilles herds (n = 70) of the Quebec–Labrador peninsula (Canada) for 1988 (data from Crête and Huot 1993), 2001, and 2002.

	Herd			Population size (low vs. high)		
Dependent variables	Estimate ± SE	$F_{[1,65]}$	p	Estimate ± SE	$F_{[1,65]}$	p
Carcass mass (kg)	–0.9±1.2	0.6	0.444	–7.9±1.2	43.9	<0.001
Body fat (%)	–2.3±0.4	39.4	<0.001	–2.8±0.4	59.8	<0.001
Protein mass (kg)	–0.2±0.3	0.7	0.411	–1.5±0.3	29.7	<0.001

Note: Reference values are the Feuilles herd and low population size (<500 000 caribou). Interactions were not significant (all p values ≥0.158) and were removed.

Table 3. Mixed model parameter estimates (means ± SE; year: random factor; season and herd: fixed factors) of body condition of lactating female caribou (*Rangifer tarandus*) from the Rivière-George and the Rivière-aux-Feuilles herds in summer (n = 51) and fall (n = 51) of 2001 and 2002 (Quebec–Labrador peninsula, Canada).

	Season			Herd		
	Estimate ± SE	$F_{[1,98]}$	p	Estimate ± SE	$F_{[1,98]}$	p
Body mass (kg)	–8.0±1.5	27.4	<0.001	9.8±1.5	40.5	<0.001
Carcass mass (kg)	–9.7±0.9	118.9	<0.001	6.7±0.9	56.5	<0.001
Body fat (%)	–5.3±0.3	275.5	<0.001	0.5±0.3	2.5	0.119
Protein mass (kg)	–1.8±0.2	67.3	<0.001	1.3±0.2	34.9	<0.001

Note: Reference values are the fall season and the Feuilles herd. Interactions were not significant (all p values ≥0.176) and were removed.

mass of calves in spring. Back-fat depths were recorded at several places along a cut made anterior from the base of the tail at an angle of 45° from the spine (Parker 1980, 1981).

Rumen content samples were washed with water through a 2 mm mesh sieve, fixed in 10% formaldehyde, and kept at room temperature until chemical analyses. Samples were oven-dried at 50 °C and ground before analysis. Nitrogen of dried rumen content was determined in duplicate by the Kjeldahl method, and results were multiplied by 6.25 to estimate percentage of protein contents, which were used as a proxy for diet or range quality in the previous few days before collection (Lewis 1994; Simard et al. 2008).

Vegetation and climate

We used NDVI to assess forage availability in early summer. This remote-sensing index has been used to describe arctic vegetation (Boelman et al. 2005) and to assess its influence on ungulate life-history traits (Pettorelli et al. 2005, 2007). We used NDVI averages in June (AVHRR data from several 8 km × 8 km pixels) for the summer ranges of both herds (http://islscp2.sesda.com/ISLSCP2_1/html_pages/islscp2_home.html; Tucker et al. 2005). Summer ranges included calving grounds and were delineated according to satellite radio-tracking data (S. Couturier, unpublished data). Weather data from the Meteorological Service of Canada for the Kuujjuaq station (58°06′N, 68°25′W) were used to compute annual means of snowfall in winter (December–March) and degree-days in July. We used the winter (December–March) NAO index (http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html; Hurrell 1995) to describe continental climate. The NAO is a large-scale fluctuation in atmospheric mass between the subtropical and the subpolar North Atlantic regions. High NAO values in Quebec–Labrador indicate cold and dry winters, as NAO from 1973 to 2003 was negatively correlated with snowfall (r = –0.529) and minimal temperature (r = –0.420) in winter (Couturier et al. 2009).

Statistical analyses

General linear mixed models (GLMM) with year as a random factor were fitted on body-condition variables to test for herd, season, and herd-size effects (fixed). The effects of vegetation and climate covariates on fall body condition were also investigated by GLMM (year: random). Each covariate was tested one at a time to avoid overparametrization as in Reimers et al. (2005). All analyses were performed with SPSS version 11 for Macintosh OS X (SPSS Inc., Chicago, Illinois, USA). Differences were considered significant at α = 0.05 and means are presented with their standard error (±SE) unless otherwise stated.

Results

We studied the nutrition of lactating female caribou using body-condition data of 80 animals collected in the summer and 121 collected in the fall (Table 1). The winter nutrition of pregnant female caribou was investigated using 65 animals collected in spring between 1984 and 2002 from the George herd. The spring data were compared with previous results obtained by Drolet and Dauphiné (1976) and Parker (1981) in 1976 and 1980, respectively (Table 1). We also compared fall and following spring data to estimate overwinter variations.

Table 4. Body condition (mean ± SE, with sample size *n* in parentheses) of reproductively active female caribou or reindeer (*Rangifer*

	Body mass (kg)			Carcass mass (kg)			Body fat (%)
Herd and years	Fall	Spring	%	Fall	Spring	%	Fall
George							
1983–1984	91.7±1.9 (15)	83.9±1.4 (13)	–9	64.3±1.5 (15)	57.9±1.1 (13)	–10	5.1±0.7 (15)
1985–1986	95.5±4.6 (4)	87.0±2.4 (12)	–9	67.0±2.7 (4)	61.3±1.6 (12)	–9	8.4±0.3 (27)
1986–1987	95.1±3.0 (17)	94.4±4.4 (15)	–1	65.0±1.8 (16)	60.7±3.0 (18)	–7	8.4±0.3 (16)
2001–2002	98.2±1.6 (14)	88.9±1.7 (17)	–10	63.9±0.9 (14)	57.0±1.5 (17)	–11	6.9±0.3 (14)
Beverly	82.0±0.6 (196)	83.0±0.4 (502)	+1				10.8±0.1 (195)
Qamanirjuaq	89.8 (38)	74.4 (64)	–17				15.6
Porcupine	91.4±2.3 (14)	88.5±2.2 (17)	–3	54.1±1.2 (14)	54.8±1.2 (17)	+1	4.6±0.5[a] (14)
Central Arctic	89.9±3.3 (5)	68.5±3.0 (6)	–24	74.7±2.9 (5)	60.7±2.6 (6)	–19	7.2±2.2 (3)
Arctic (Alaska)	89.5 (20)	75.0 (102)	–16				
Nelchina	106.5 (14)	104.5 (55)	–2				
Alaska peninsula	103.5 (7)	105.5 (6)	+2				
Finnmark	68.5±0.8 (79)	65.7±0.8 (79)	–4	28.4±1.5 (9)	28.5±1.8 (9)	0	
Hardangervidda[b]				25.3±0.9 (14)	23.8±0.6 (20)	–6	
Knutshø[b]				43.3±3.3 (7)	39.9±1.1 (9)	–8	
Forelhogna[b]				46.8±1.9 (7)	41.9±2.0 (9)	–10	
Coats Island	87.3±2.5 (7)	84.9±3.3 (8)	–3	51.3±1.8 (7)	38.7±1.4 (8)	–25	14.3[a] (5)
Southampton I.				72 (8)	69 (38)	–4	7.8 (8)
Svalbard			–50				
South Georgia							

[a]In these studies, body fat is in kilograms
[b]No data were available for the fall, thus comparisons were made between February and April.
[c]Muscle mass in kilograms.
[d]Estimated from changes in kidney-fat mass.

Table 5. Body condition (mean ± SE, with sample size *n* in parentheses) in the spring for pregnant female caribou (*Rangifer tarandus*) and calf mass from the Rivière-George herd, Quebec–Labrador peninsula, Canada.

Sampling dates	Body mass (kg)	Kidney fat (g)	Back fat (mm)	Calf mass (kg)	Reference
March 1976	101.8±1.7 (21)		28.4±1.7 (21)	56.1±0.6 (3)	Drolet and Dauphiné 1976
3–15 April 1980	93.4±0.8 (103)[a]	79.8±3.3 (81)		47.5±0.8 (29)	Parker 1980, 1981
14–16 April 1984	83.9±1.4 (13)	38.6±3.6 (13)	5.9±1.8 (13)	44.2±2.1 (9)	Huot 1989
14–22 March 1986	87.0±2.4 (12)	55.9±7.6 (12)	12.6±3.9 (10)	38.6±1.5 (13)	This study
5–14 April 1987		37.9±2.9 (23)	1.2±0.6 (18)		This study
25–27 April 1997				40.6±1.4 (14)	This study
4–14 March 2002	88.9±1.7 (17)	40.9±6.2 (16)	9.1±2.0 (16)	42.4±1.4 (22)	This study

[a]This sample of 103 adult females includes 6 nonpregnant females.

Summer and fall nutrition

All variables indicated that the summer body condition of the Feuilles females was better than that of the George females in 1988, while it was the opposite in 2001 and 2002 (Fig. 1). We assessed the effects of herd identity and population size on summer body condition using carcass mass, body fat, and protein mass (no body mass data in 1988). Only body fat was significantly different between herds with females from the Feuilles herd in better condition than those of the George herd, while all three variables were significantly influenced by herd size (Table 2). Summer condition was lower during population highs as predicted by H_1. Both herds reacted similarly to population-size variations, as the interaction herd × population size was not significant (p values ≥0.158).

Protein in summer rumen contents was higher in the Feuilles herd than in the George herd in 1988, while it was the opposite in 2001 and 2002 (Fig. 1). After controlling for the factor year (random), rumen protein in 2001 and 2002 was 1.6% ± 0.5% ($F_{[1,48]}$ = 8.6, p = 0.005) higher in the George herd than in the Feuilles herd in summer, but there was no difference between the two herds in the fall ($F_{[1,46]}$ = 2.9, p = 0.093).

To assess variations in body condition from summer to fall in the two herds, we used only data from 2001 (n = 44) and 2002 (n = 58) because we had no other fall data for the Feuilles herd (Table 1). Season and herd influenced body, carcass, and protein masses (p values <0.001; Table 3). For body fat, season was significant (p < 0.001), but there was no difference between herds (Table 3). Body mass increased 8.0 ± 1.5 kg from summer to fall, while females from the George herd were 9.8 ± 1.5 kg heavier than those from the Feuilles herd. Similarly, carcass mass was 9.7 ± 0.9 kg higher in the fall than in the summer, while females from the George herd were 6.7 ± 0.9 kg heavier than those from the Feuilles herd. In the fall, protein mass was 1.8 ± 0.2 kg higher than in the summer and 1.3 ± 0.2 kg higher in the George herd than in the Feuilles herd. Body fat increased *tarandus*) in the fall (lactating) and the spring (pregnant) and relative overwinter changes (%).

		Protein mass (kg)			
Spring	%	Fall	Spring	%	Reference
9.9±0.5 (13)	+94	17.4±0.4 (15)	17.0±0.3 (13)	–2	This study
12.9±1.3 (10)	+54	17.0±0.3 (30)	14.6±0.3 (12)	–21	This study
10.4±0.4 (21)	+24	16.1±0.3 (19)	15.7±0.3 (23)	–2	This study
13.7±1.1 (7)	+99	17.3±0.3 (14)	16.0±0.5 (7)	–8	This study
12.0±0.1 (498)	+11				Thomas and Kiliaan 1998
12.4	–21				Dauphiné 1976
6.1±0.3[a] (17)	+33	10.2±0.3 (14)	9.5±0.2 (17)	–7	Chan-McLeod et al. 1999
6.3±0.7 (5)	–13	17.9±0.4 (3)	13.8±0.7 (5)	–23	Gerhart et al. 1996
					Skoog 1968
					Skoog 1968
					Skoog 1968
					Tyler et al. 1999
					Skogland 1984
					Skogland 1984
					Skogland 1984
2.3[a] (8)	–84	6.3 (5)	2.7 (8)	–57	Adamczewski et al. 1993
8.6 (38)	+10	34.0[c] (15)	32.0[c] (45)	–6	Ouellet et al. 1997
	–76			–31	Reimers et al. 1982
	–83[d]				Leader-Williams and Ricketts 1982

5.3% ± 0.3% from the summer to the fall. There was no season × herd interactions (p values >0.176).

Population size (high in 1983–1987 and low in 2001–2002) of the George herd did not affect body mass, carcass mass, protein mass, and body fat in the fall (p values ≥0.221). We assessed the effects of NDVI in June, degree-days in July, snowfall, and NAO on fall body condition. None of these covariates affected body mass, carcass mass, and body fat (p values ≥0.083). However, protein mass increased by 0.6 ± 0.2 kg for each increment of 0.1 unit of NDVI in June ($F_{[1,8]} = 6.9$, $p = 0.032$). No other covariate affected protein mass (p values ≥0.191).

Winter nutrition

We assessed how condition changed from fall to spring during four winters between 1983 and 2002 in the George herd. Body, carcass, and protein masses were significantly higher in the fall than in the spring, respectively, by 6.2 ± 1.9 kg ($F_{[1,103]} = 10.5$, $p = 0.002$), 5.5 ± 1.4 kg ($F_{[1,99]} = 15.8$, $p < 0.001$), and 1.1 ± 0.3 kg ($F_{[1,129]} = 17.6$, $p < 0.001$). However, in support of H_2, body fat was 4.1% ± 0.4% ($F_{[1,119]} = 95.0$, $p < 0.001$) higher in the spring than in the fall and the same trend was observed in all winters studied (Table 4, George). Absolute values of body-fat masses (in kg) also increased from fall to spring (computed from means presented in Table 4). Protein in the rumen of females from the George herd decreased over winter from 8.0% ± 0.2% ($n = 14$) in October 2001 to 5.2% ± 0.3% ($n = 8$) in March 2002 ($t_{[20]} = 7.5$, $p < 0.001$). Herd size (high in 1984–1987 and low in 2002) did not affect body, carcass, and protein masses in the spring (p values ≥0.210, $n \geq 55$; Table 4, George), but body fat was 2.9% ± 1.1% ($F_{[1,49]} = 6.7$, $p = 0.013$) higher when herd size was low. We also compared our spring condition data with studies done in 1976 and 1980 on the George herd, and found that condition had generally declined but appeared to be recovering in 2002 (Table 5).

Female productivity

The pregnancy rate of females from the George herd was generally high before 1981. It decreased substantially in 1986–1987 and 1992 when population size was high, but seemed to be increasing again in 2001–2002 (75%; Fig. 2). The pregnancy rate of the Feuilles herd was estimated for the first time in 2001–2002, and it was very low (52%; Fig. 2).

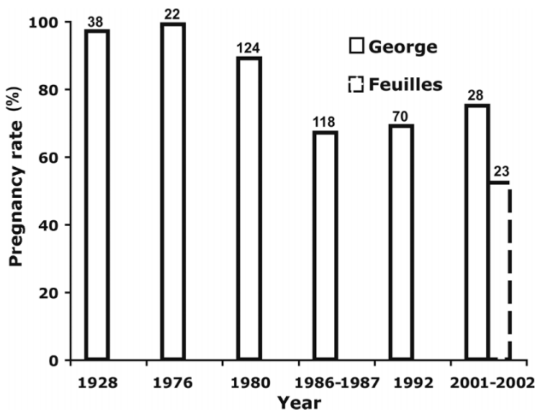
Discussion

We confirmed our first hypothesis that body condition in summer and spring was negatively related to herd size. Our second hypothesis was partly supported, as females from the George herd gained fat in winter, both in relative and absolute terms, contrary to most northern ungulates. NDVI in June affected body protein in the fall, confirming our third hypothesis and the prominent influence of summer range on caribou body condition.

The influence of herd size or density dependence

It has been shown that population size is negatively related to condition in ungulates, particularly in studies involving juveniles (e.g., Fergusson et al. 2000; Forchhammer et al. 2001; Kjellander et al. 2006; Toïgo et al. 2006), but also adults (e.g., Bonenfant et al. 2002; Pettorelli et al. 2002). In a classical density-dependent response, an increase

Fig. 2. Pregnancy rates (%) of females from the Rivière-George (George) and the Rivière-aux-Feuilles (Feuilles) caribou (*Rangifer tarandus*) herds of the Quebec–Labrador peninsula (Canada). Pregnancy status was estimated from the presence–absence of a fetus during spring necropsies or from a pregnancy-specific protein B (PSPB) assay for live-captured animals. Sample sizes are shown on top of the bars. Data from the following sources — 1928: Strong (1930); 1976: Bergerud (1980); 1980: Parker (1981); 1986–1987: Couturier et al. (1990); 1992: Crête et al. (1996); and 2001–2002, this study.



in population size over time leads to deterioration in animal condition. Density dependence is a commonly observed process in ungulates that affects many life-history traits mostly through its influence on body condition (Sæther 1997; Gaillard et al. 2000). We have reported elsewhere (Couturier et al. 2009) that birth mass in the George and Feuilles herds were both inversely related to herd size. We found here that density dependence is also acting on adults, and the negative relationship between herd size and body condition in summer supports H_1 (Table 2). In the late 1980s, females from the Feuilles herd were in better condition in summer than those from the George herd that was then near peak population size. In 2001 and 2002, however, it was the opposite and the females from the Feuilles herd were in lower condition, but the Feuilles herd was also larger then. These changes in summer condition were mirrored in diet-quality variations estimated from protein in rumen contents, suggesting that the George summer range was likely of better quality than that of the Feuilles range in 2001–2002. Our spring condition data also supported H_1 but only for body fat or when comparing our results to data collected in 1976 or 1980. Body mass (–18%), kidney-fat mass (–53%), back fat (–96%), and calf mass (–31%) all declined from 1976–1980 to 1984–1987. This decline in spring body condition confirmed that the condition of females from the George herd rapidly decreased when the herd was still increasing, suggesting that density-dependent effects might become evident before a population reaches its carrying capacity. This suggests that our arbitrary threshold of 500 000 animals to identify a large herd is conservative, as some impacts of herd size may occur at lower population size. The fall condition data collected from 1983 do not support H_1, perhaps because most of the changes occurred earlier. We have shown elsewhere that lower jaw length from the George herd declined between the 1960s and the early 1980s (Couturier 2007).

Gaining fat in winter

Seasonality is a dominant feature of the boreal environment to which animals respond both behaviorally and physiologically. Intrinsic cycles of growth and fattening appear to be adaptations to seasonal environments in which animals are confronted with long, predictable periods of potential undernutrition (Tyler and Blix 1990). Many northern ungulates are experiencing a strong winter decrease in condition, losing 15%–30% of their body mass (moose (*Alces alces* (L., 1758)): Franzmann et al. 1978; white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)): Taillon et al. 2006; bighorn sheep (*Ovis canadensis* Shaw, 1804): Festa-Bianchet et al. 1996). White-tailed deer on Anticosti Island, for example, accumulated large fat deposits, but the body fat dropped from 15% of total body mass in the fall to only 1% by mid-April (Huot 1982). On Coats Islands, body fat of caribou declined from 14.3 kg in November to 0.8 kg in June (Adamczewski et al. 1993).

Spectacular examples of overwinter declines in body condition might explain why the winter loss of condition became a common observation that has not often been challenged. Contrary to this situation, however, we showed that the percentage of body fat increased over winter and we suggest that it is likely because of inadequate summer nutrition. Huot (1989) noted that individuals from the George herd accumulated only limited fat reserves in summer and raised the possibility that energy was deficient because of the poor summer habitat. He showed that calves, yearlings, and adult females gained fat over winter and suggested that George caribou were more affected by protein deficiency than by a negative energy balance from October to April. We found that body condition improved from summer to fall (Table 3), but this gain was probably insufficient. We suggest that fat levels may be below a set point in the fall so that lipogenesis continues in winter. The body, carcass, and protein masses did not decrease much through winter, suggesting that these condition indices likely reached their set point in the fall, which may not be the case for the more variable fat reserves (Table 4; Ouellet et al. 1997). Evidence for set points in condition have been reported in mule deer (*Odocoileus hemionus* (Rafinesque, 1817); Renecker and Samuel 1991) and caribou (Adamczewski et al. 1987). In ruminants, energy is allocated first to maintenance, then to protein deposition, and finally to lipogenesis (Chan-McLeod et al. 1999). It is then possible that caribou in our study reached a set point in protein in the fall but not in fat reserves. Although the need to increase fat reserves over winter is likely generated by the deterioration of summer habitat, we suggest that gaining fat in winter is made possible by a good winter habitat. Arseneault et al. (1997) confirmed the abundance of lichens in the George and Feuilles winter ranges. However, they also reported that caribou numbers exceeded the carrying capacity of lichens between 1989 and 1992. More studies are needed to assess the current condition of winter ranges.

From the literature on the genus *Rangifer*, we compiled data on overwinter changes in body condition (Table 4). Even if estimation methods may vary among studies, most data showed that body, carcass, and protein masses remained stable or declined over winter. In some studies, body fat followed the same pattern. However, individuals from the George, Beverly, Southampton, and Porcupine herds increased fat reserves over winter. Females from the Porcupine herd reached 4.6 kg of fat in November–December and 6.1 kg in March–April (Chan-McLeod et al. 1999). When expressed in percentage of body mass, these fat reserves increased from 5.0% to 6.9%. Most studies expressed fat as a percentage of body mass so that the absolute fat mass may decrease while its percentage increases. However, the magnitude of changes in percentage of fat was large, while body mass did not vary much over winter in those herds, so that both absolute and relative fat levels increased over winter. The George herd is remarkable because fat levels increased by as much as 99% from fall to spring. Crête and Huot (1993) suggested that the George summer range was prone to overgrazing because of its relatively small size. This was confirmed by Bergerud (1996) who computed caribou densities above the treeline for eight herds. The four highest densities were George (13.8/km^2), Porcupine (4.4/km^2), Qamanirjuaq (2.3/km^2), and Beverly (2.2/km^2) herds. Individuals of three of these four herds increased fat reserves from fall to spring (Table 4), suggesting that grazing on the summer range may have a density-dependent effect on fall condition, and subsequently, on the need to continue lipogenesis in winter. Like Schmelzer and Otto (2003), we suggest that a good winter range partly compensated for the summer forage limitation of the George herd. Resulting demographic consequences of poor summer habitat in the 1980s were reduced pregnancy rate (Fig. 2), as well as decreased recruitment and survival (Crête et al. 1996). Mahoney and Schaefer (2002) suggested similar demographic impacts of density-dependent competition for summer forage in Newfoundland caribou. Our results do not refute the well-documented observation that body condition of northern ungulates deteriorates in winter, but they illustrate that this process is more complex than previously thought. Summer nutrition is essential for the accumulation of body reserves (Stewart et al. 2005) and more emphasis should be given to study its effects on northern herbivores (Therrien et al. 2007).

Vegetation and climate

We found no impact of climate covariates on body condition (H_3). However, NDVI had a positive effect on the protein mass in the fall. In a study of calf-mass variations in the George and Feuilles herds (Couturier et al. 2009), NDVI in June was the most prominent covariate and influenced positively calf body mass at birth and at 135 days old. An early and gradual start to the plant growing season provides better nutrition for a long period, and probably explains the positive effect of NDVI on the condition of females and their calves (Pettorelli et al. 2007). A significant warming between 1973 and 2003 was reported for the month of May in our study area and the NDVI effect was mediated through climate warming as May degree-days were correlated with NDVI in June (Couturier et al. 2009). Myneni et al. (1997) reported that spring temperature warming in Nordic regions has resulted in earlier plant growth and NDVI increases.

Relationships between reproduction and body condition

Facing the reproduction dilemma, female ungulates may use different strategies to cope with poor foraging conditions. First, capital breeders such as caribou or bighorn sheep accumulate body reserves during periods of forage abundance and use these reserves to reproduce when the conditions are difficult (Festa-Bianchet et al. 1998). Second, income breeders such as western roe deer (*Capreolus capreolus* (L., 1758)) can meet the energy costs of reproduction by using higher quality habitats (Pettorelli et al. 2002). Finally, female ungulates can also adjust their reproductive effort to poor foraging conditions by skipping a reproductive season (Cameron 1994; Côté and Festa-Bianchet 2001) to help replenish their body condition. These strategies can smooth the effects of poor nutrition on the body condition of adult females and can mask annual variations.

An alternate hypothesis, therefore, could be that mothers gave less resource to their calves, buffering the effects on their own condition (Therrien et al. 2007, 2008). In support of this selfish mother's hypothesis, the negative influence of herd size on calves' birth mass was strong (Couturier et al. 2009). Moreover, females may have also buffered the detrimental effects of competition by skipping a reproductive season, therefore reducing the herd productivity and not contributing to our sample of body condition of reproductive females. It has been shown that females of the George herd must reach a body fat threshold of 7.8% in the fall to become pregnant (Crête et al. 1993). From 1983 to 2001, our results showed that body fat in the fall varied between 5.1% and 8.4% for females of the George herd (Table 4). Until 1980, nearly all females were pregnant (Fig. 2) when the George herd was under 300 000 caribou and probably not yet under severe nutritional stress. However, herd growth continued and pregnancy rate fell in the late 1980s. Annual fall recruitment for the George herd also decreased and averaged only 31 calves/100 females in 1990–2003 (Couturier et al. 2004).

Implications for management and conservation

Wildlife management strategies should be based on reliable population-size estimates, but for many free-ranging mammals, this is not possible. When faced with the difficulty of getting reliable population estimates, population censuses should be replaced by ecological studies that focus on habitat quality in relation to factors that affect body condition, reproduction, and survival to predict population trends (Thomas 1998; Morellet et al. 2007). Body and carcass mass along with indices of fat and protein reserves appear to be useful parameters to assess the dynamics of body condition and its influence on other life-history traits, such as reproduction (Sæther 1997). Adult body-condition studies like here or adult body-size monitoring (Couturier 2007; Hewison et al. 1996) are perhaps of greatest value for long-term monitoring of population trends, whereas variations in juvenile body mass (Couturier et al. 2009; Toïgo et al. 2006) may be more informative of annual variations, at least for ungulate populations that are food-limited. Non-nutritional elements of habitat quality such as predators and parasites, however, should also be considered.

Acknowledgements

This study was funded by the Gouvernement du Québec, Newfoundland and Labrador Government, Institute for Environmental Monitoring and Research, Fonds pour les espèces nordiques – Fondation de la faune du Québec, National Defense (Canada), Hydro-Québec, Caribou Québec, Makivik, and the Natural Sciences and Engineering Research Council of Canada. The 1988 and 1993 summer data were collected by M. Crête and M. Manseau, respectively. We thank everyone who particiated in the field and laboratory work, especially D. Fiset, J.Y. Lacasse, L. L'Italien, N. Lizotte, and G. Picard. Comments from C. Barrette, P. Kjellander, S. Payette, and J.A. Schaefer greatly improved the manuscript.

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