

Variation in body condition of migratory caribou at calving and weaning: Which measures should we use?¹

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Abstract: Monitoring the body condition of ungulates is often considered an efficient way to assess habitat quality. It is therefore essential to select adequate measures to describe individual body condition. Because there is no consensus on which measurement(s) can best describe individual variability in body condition, field biologists often measure several variables, increasing processing time. From 2007 to 2009, we assessed body condition of female-calf pairs in 2 herds of migratory caribou in Northern Quebec/Labrador, Canada, using multiple measurements of size, mass, and fat depth. We sought to identify, using multivariate analysis, which measurement(s) had the greatest influence on a composite measure of body condition of females and calves at calving and weaning. Our results indicate that adult females are best described with a body bulkiness index opposing heavy and long/round-bodied females with high body protein reserves to light and short/slender-bodied females with low body protein reserves. At weaning, adult females can also be differentiated by a body fat index opposing fat to lean females. Calf body condition is best described by mass at birth and by a combination of mass and size measurements at weaning, opposing heavy and tall individuals with high protein reserves to light and short ones with low protein reserves. Overall, body mass appears to be the measurement that best describes individual variability in body condition of females and calves at calving and weaning. Our systematic comparison of body condition measurements will provide field biologists with guidance for future data collection.

Keywords: body condition, body fat, body mass, body size, migratory caribou.

Résumé : Le suivi de la condition corporelle chez les ongulés constitue un outil privilégié pour évaluer la qualité d'un habitat et son influence sur la survie et le potentiel reproductif. Il est ainsi essentiel d'identifier les mesures décrivant adéquatement la condition corporelle des individus. En général, les biologistes mesurent de nombreuses variables, sans toutefois qu'un consensus soit établi sur la ou les mesures décrivant le mieux la condition corporelle des individus. De 2007 à 2009, nous avons évalué la condition corporelle de paires de femelle-faon de deux troupeaux de caribous migrants du Nord du Québec/Labrador, Canada, en récoltant diverses mesures individuelles de taille, de masse et de réserves corporelles. Notre objectif était d'identifier, à l'aide d'analyses multivariées, la ou les mesures ayant la plus grande influence sur une mesure composite de condition corporelle pour les femelles et les faons à la mise bas et au sevrage. Nos résultats indiquent que les femelles adultes sont départagées par un indice de corpulence opposant les femelles lourdes, longues et rondes avec des réserves protéiques élevées, aux femelles légères, courtes et minces avec de faibles réserves protéiques. Au sevrage, les femelles adultes sont aussi départagées par un indice de gras corporel opposant les femelles grasses aux femelles maigres. La condition corporelle des faons est décrite par la masse à la naissance et par une combinaison de mesures de masse et de taille corporelle au sevrage opposant les faons lourds et grands avec des réserves protéiques élevées, aux faons légers et courts avec de faibles réserves protéiques. Globalement, la masse corporelle explique la plus grande variabilité de la condition corporelle pour toutes les périodes et les classes d'âge. Notre comparaison systématique de mesures de la condition corporelle guidera les biologistes dans leurs récoltes de données futures.

Mots-clés : caribou migrateur, condition corporelle, masse corporelle, réserves de gras, taille corporelle.

Nomenclature: ITIS, 2011.

Introduction

Body condition usually refers to the amount of energy reserves available to sustain basal metabolism and daily and seasonal activities (Barboza, Parker & Hume, 2009; Parker,

Barboza & Gillingham, 2009). Individual body condition can vary according to access to and availability and quality of food, which are mostly influenced by population density and weather for herbivores (Bonenfant *et al.*, 2009; Parker, Barboza & Gillingham, 2009), and energetic expenses for daily and seasonal activities (Barboza, Parker & Hume, 2009). Body condition also depends on intrinsic characteristics of individuals, such as genotype, age, sex, and

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reproductive status (Hewison *et al.*, 1996; Festa-Bianchet, Gaillard & Jorgenson, 1998; Barboza & Parker, 2008). Juveniles have higher rates of protein turnover and skeletal growth compared to adults (Barboza, Parker & Hume, 2009) and, consequently, face important trade-offs in allocating metabolic resources to body growth, maintenance, and energy storage for survival. Adults, on the other hand, must allocate energy to current and future reproduction, maintenance, and energy storage for survival. Adult males and females differ, moreover, in reproductive effort, nutritional requirements, and metabolic rate (Barboza, Parker & Hume, 2009) and may respond differently to environmental conditions (Toigo *et al.*, 2006; Pérez-Barberia *et al.*, 2008).

Good body condition has been related to greater adult size (Hewison *et al.*, 1996), earlier reproduction (Festa-Bianchet, Gaillard & Jorgenson, 1998), and higher fecundity and survival rates (Festa-Bianchet *et al.*, 1997; Gaillard *et al.*, 2003) in several ungulates. Monitoring body condition is often considered an efficient way to assess habitat quality (Morellet *et al.*, 2007; Bonenfant *et al.*, 2009). To link body condition to habitat quality, however, it is essential to select an adequate measure to describe individual body condition. Ideally, we require a metric that can quantify as much inter-individual variability as possible using the minimum number of measurements. Using a minimum number of measurements enables researchers to better focus their sampling methods and decreases handling time of live animals. The metric should also be sensitive to changes in resource availability that may affect sex and age classes differently. Because there is often no consensus on the measurement(s) needed to adequately assess individual variability in body condition, field biologists often measure several variables without being certain of their usefulness.

In ungulates, several measurements of body mass, body size, and body reserves such as fat and proteins have been used to describe individual body condition, with some uncertainty on which metrics should be prioritized. Mass is the most commonly used index to describe seasonal variations in body condition (Barboza, Parker & Hume, 2009; Parker, Barboza & Gillingham, 2009) and assess cohort effects and annual changes in environmental conditions (Hewison *et al.*, 1996; Lesage *et al.*, 2001; Gaillard *et al.*, 2003). Body mass integrates several body condition components, such as variations in protein and fat reserves, but it may not detect subtle but meaningful responses to environmental factors (Dale *et al.*, 2008; Parker, Barboza & Gillingham, 2009; Simard *et al.*, 2010) and cannot differentiate among changes in body size, fat, and protein reserves (Schulte-Hostedde *et al.*, 2005; Simard, 2010). Attempts to correct body mass for structural size (Schulte-Hostedde *et al.*, 2005; Toigo *et al.*, 2006) have had limited success (Jakob, Marshal & Uetz, 1996; Green, 2001). Bones can be measured to assess skeletal size (Huot, 1988), and may provide information on the environmental conditions experienced by individuals at birth and during growth (Gaillard *et al.*, 2003; Barboza, Parker & Hume, 2009). Some bones, however, have a higher growth priority than other tissues (Klein, 1964). Therefore, skeletal size is not as sensitive as body mass or body fat to changes in resource availability, and may respond only to long-term environ-

mental pressures (Klein, Meldgaard & Fancy, 1987; Toigo *et al.*, 2006; Couturier *et al.*, 2010). Body fat is widely considered to be the major energy store (Barboza, Parker & Hume, 2009) and is generally used to relate body condition to reproductive success (Chan-McLeod, White & Russell, 1999) or to estimate critical levels of body condition that may affect survival, for example by measuring bone marrow fat (Cerderlund *et al.*, 1989; Parker, Barboza & Gillingham, 2009). Individual responses to seasonal environmental factors and reproductive activity have also been measured by changes in protein reserves in species such as *Rangifer* (Parker, Barboza & Gillingham, 2009) and *Odocoileus* (Simard *et al.*, 2010). The choice of the best metric to answer a research question, therefore, is not straightforward (Cook *et al.*, 2001).

Here, we report on an extensive sampling of body condition of migratory caribou (*Rangifer tarandus*) female-calf pairs, based on multiple measurements of size, mass, and fat depth for each individual. Most studies on large ungulates have used 1 or a few specific body condition measurements, assuming that the chosen measurement(s) would suffice to differentiate body condition among individuals. In our study, we had the opportunity to contrast and compare several body condition measurements that are commonly used to represent body mass, body size, or body fat of individuals. We sought to identify, using multivariate analysis, which measurement(s) had the greatest influence on a composite measure of body condition of females and calves at calving and weaning, 2 periods crucial for juvenile growth and survival. We expected that the measurement(s) explaining most variability in the multivariate analysis would differ between age classes and seasons: body size should vary more in growing calves than in adult females that have reached their adult size, while body fat measurements should be more variable at weaning than at calving, when body fat reserves are usually depleted in caribou. In addition, we assessed which body size measurements provide direct information on the skeletal size of an individual. Finally, we made specific suggestions as to which measurements to collect to efficiently describe body mass, body size, and body fat of individuals.

Methods

STUDY AREA

Two large herds of migratory caribou inhabit Northern Quebec and Labrador: the Rivière-George herd (RG) and the Rivière-aux-Feuilles herd (RAF) (Boulet *et al.*, 2007). These herds range over nearly 1 million square kilometres and travel up to 6000 km yearly across taiga and tundra. The 2 herds are not genetically different (Boulet *et al.*, 2007), but they differ in body condition, movement rates, and demography (Couturier *et al.*, 2010). Over the last few decades, these 2 herds have shown large fluctuations in size, recruitment rates, and individual body condition. The RG herd increased from about 5000 caribou in the 1950s (Banfield & Tener, 1958) to more than 775 000 in 1993 (Couturier *et al.*, 1996), then declined to approximately 385 000 in 2001 (Couturier *et al.*, 2004) and 74 000 in 2010 (Quebec Government aerial count). The RAF herd

increased from 56 000 caribou in 1975 (Le Hénaff, 1976) to at least 628 000 in 2001 (Couturier *et al.*, 2004). Although there are no recent estimates, the RAF herd is thought to be currently much larger than the RG herd.

RANGE USE

At calving, females of the RG herd aggregate on the high tundra plateaus on the eastern Quebec–Labrador Peninsula (57° N, 65° W). More than 800 km away, females of the RAF herd calve in the centre of the Ungava Peninsula (61° N, 74° W). Females are highly philopatric, and over 93% return to their traditional calving grounds each year (Boulet *et al.*, 2007). Summer ranges are larger than calving grounds and are used during lactation, from early July to mid-September. Migration from summer range to winter range occurs in early fall, at the time of physiological weaning and before the breeding season (Lavigne & Barrette, 1992). The migration and seasonal ranges of the RG and RAF herds have been monitored since 1986 using caribou fitted with radio-collars (Couturier *et al.*, 2004). There is no overlap in the calving grounds and summer ranges used by the 2 herds (Couturier *et al.*, 2004).

BODY CONDITION DATA COLLECTION

During the calving and weaning periods of 2007 to 2009, we collected female–calf pairs from both herds (Table I.) At peak calving (6–14 June), pairs were located by helicopter. Pairs were collected throughout the entire calving grounds (calving ground size: RG = 6500 ± 745 km²; RAF = 54 500 ± 2700 km²), and collection sites were separated by several kilometres (RG: calving: 21 ± 3 km, weaning: 64 ± 9 km; RAF: calving: 83 ± 12 km, weaning: 147 ± 27 km). Calves were reliably matched to females because mothers separate from the herd at parturition. Only females with a newborn calf (less than 2 days old) were sampled. Newborns were unsteady and unable to run, their hoof pads barely worn, their fur wet or newly dried, and their umbilical cord still attached (Adams, 2005; Couturier *et al.*, 2009a). At weaning (October–November; Table I), groups of caribou were located by helicopter and female–calf pairs were identified using behavioural observations on the ground. Within groups, calves stayed in immediate proximity to and interacted frequently with their mothers, making identification of pairs certain. We collected pairs over the entire range covered by animals fitted with satellite radio-collars and spaced out collections by several kilometres (RG: 64 ± 9 km; RAF: 147 ± 27 km). All animals were culled to collect the totality of body condition measurements.

TABLE I. Sampling dates and sample sizes of female–calf pairs of migratory caribou from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, Northern Quebec and Labrador, Canada.

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

We collected the following measurements from adult females at calving and weaning and calves at weaning: total body mass (kg), dressed body mass (kg), total body length (cm), hind foot length (cm), chest girth (cm), mandible length (cm), femoral bone length (cm), peroneus muscle mass (g), rump fat (mm), kidney fat (%), and femoral bone marrow fat (%). Mandible and femoral bone length were only measured on adult females. For newborns, we measured total body mass (kg), total body length (cm), hind foot length (cm), peroneus muscle mass (g), rump fat (mm), and kidney fat (%). We estimated the age of adult females by counting the cementum layers in incisor teeth (Hamlin *et al.*, 2000) and noted the sex of calves. Body condition measurements were collected as follows:

1. Body mass: Total and dressed mass (total body mass minus viscera and bleedable blood, *i.e.*, associated blood loss during removal of viscera) were obtained using a spring scale (± 0.25 kg). Birth mass of calves was recorded to the nearest 0.1 kg using a Pesola spring scale (Pesola AG, Baar, Switzerland).
2. Body size: Total length was measured following the dorsal perimeter of the body from the end of the upper lip to the last vertebra of the tail (± 0.2 cm), hind foot length from the calcaneum to the edge of the hoof (± 0.2 cm) along the exterior of the foot, and chest girth as the circumference behind the forelegs applying a 2-pound pull tension measured with a fish scale on the tape (± 0.2 cm). Using a calliper, we measured the length of the femur (± 0.1 mm) and the mandible from the process angularis to the anterior part of the dentary bone (± 0.1 mm). Bones were cleaned of meat prior to measuring.
3. Body fat: As body condition declines, fat stores are used sequentially beginning with subcutaneous fat, then kidney fat, and finally marrow fat (Mautz, 1978). We measured all 3. Rump fat thickness was measured at 5 cm from the base of the tail at an angle of 45° from the backbone (Leader-Williams & Ricketts, 1982). We inserted a ruler (± 0.5 mm) into the fat layer to measure its maximum thickness. Kidney fat index, the ratio of the mass of perinephric fat (± 0.5 g; not including fat extending beyond the kidney; Riney, 1960) and kidney mass (± 0.5 g), was measured using the following equation: KFI = (weight of fat around the kidneys) · (weight of kidneys without fat)⁻¹ · 100 (Huot, 1988). Femur bones were collected and frozen. About 20 g of marrow was extracted from the central portion of the bone and oven-dried at about 50 °C until its mass stabilized (Neiland, 1970). Femur marrow fat is the percentage of dry mass (%).
4. Body proteins: The peroneus muscles (*peroneus tertius* with extensor *digitorum longus* and extensor digit III) provide a good estimation of protein mass in caribou (for more details see Crête & Huot, 1993). They were extracted from the right hind leg and weighed to estimate body protein reserves with a Pesola scale (± 0.5 g; wet mass) (Huot, 1988; Chan-McLeod, White & Russell, 1995).

Animal manipulations were done in accordance with guidelines from the Canadian Council on Animal Care, and the Laval University Animal Care and Use Committee approved all procedures (#2008015-3).

STATISTICAL ANALYSES

We used principal component analysis (PCA; SAS Institute 9.2) to summarize the variation of untransformed body condition measurements separately for females and calves at calving and weaning (for details on the method see Jolliffe, 2005). Principal component analysis examines relationships among several quantitative variables and synthesizes the variance in the data along interpretable gradients (Jolliffe, 2005). It derives a small number of independent linear combinations (*i.e.*, principal components, PCs) of a set of variables that retain as much of the information in the original variables as possible. PCAs are well suited to identify variable sets related to size and shape factors (Morrison, 1967). Body condition measurements that form the main structuring process of variation in the data should occur as the first axis (PC1) and account for the larger part of observed variation in traits. Other PCs could represent additional axes of body condition variation. There are many ways to identify a cut-off value using PCAs. We used 2 of the most common criteria to assess the number of axes to extract from the PCA. We assessed the number of PCs using the scree-test method (sharp decline in consecutive eigenvalues; Cattell, 1966) and by selecting PCs with eigenvalues > 1.0 (Jolliffe, 2005). We pooled data from different years and herds to assess the relationships between body condition measurements in separate PCAs for adult females and calves. Rump fat was excluded from all PCAs as no individual had detectable rump fat at calving and only a few at weaning (see data repository at www.ecoscience.ulaval.ca). We use the expression “body condition” throughout the text to refer to variations in the different body condition measurements and PC axes. We are aware, however, that the term “body condition” should be used carefully as its often refers to the amount of energy and key elements (*e.g.*, nitrogen in protein or calcium in bone) available in stores of fat and lean tissue for maintaining body function at rest or at higher levels of activity and production (Barboza, Parker & Hume, 2009).

Measures of body condition should ultimately be used as correlates of survival, growth, or reproduction and therefore broadly reflect fitness (Parker, Barboza & Gillingham, 2009; Simard, 2010).

All data are presented as means ± SE. A level of $\alpha = 0.05$ was used to determine significance.

Results

ADULT FEMALES

At calving, body condition of adult females could be summarized by 2 PCs (consecutive eigenvalues [% variation explained]: PC1: 5.13 [51.3%], PC2: 1.27 [12.7%]) for 64% of the variation observed among body condition measurements. PC1 corresponded to a body bulkiness index opposing heavy and long/round-bodied females with high body protein reserves to light and short/slender-bodied females with low body protein reserves (for body condition measurements, see Table II, and for eigenvectors, see Table III and Figure 1a and b). PC2 corresponded to a body size index opposing tall to short females (Table II, Table III, and Figure 1a and b). Marrow fat and kidney fat measurements were not selected by the PCA (grouped under PC3: 0.86 [8.6%]).

At weaning, variation among body condition measurements of individual adult females was described by 3 PCs (consecutive eigenvalues [% variation explained]: PC1: 2.37 [23.7%], PC2: 2.21 [22.1%], PC3: 2.12 [21.2%]) for 67% of the variation observed among body condition measurements. PC1 corresponded to a body bulkiness index opposing heavy and round-bodied females with high protein reserves to light and slender-bodied females with low protein reserves (for body condition measurements, see Table II, and for eigenvectors, see Table III and Figure 1c and d). PC2 corresponded to a body size index opposing tall to short females (Table II). PC3 corresponded to a body fat index opposing fat to lean females (Table II and Figure 1c and d). PC scores and body mass of adult females also varied between herds (see data repository at www.ecoscience.ulaval.ca).

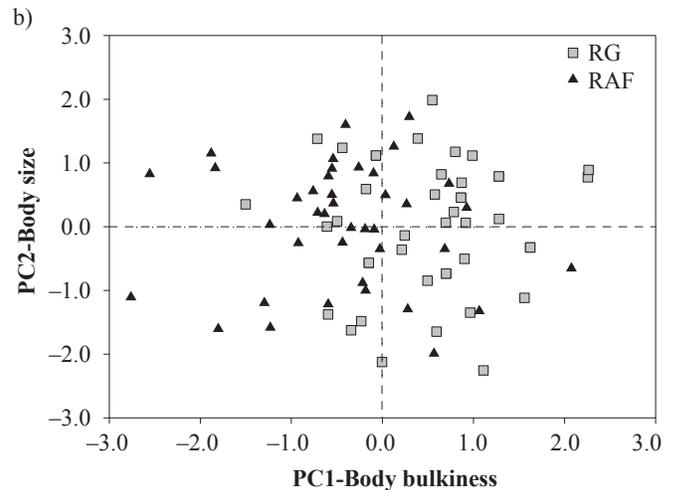
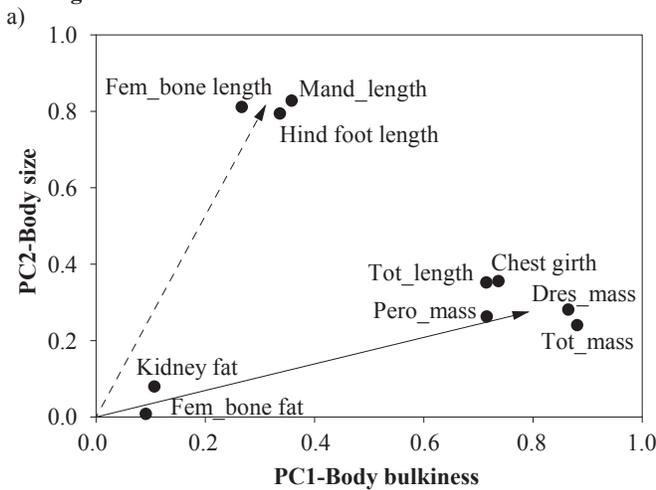
TABLE II. Body condition measurements (mean; standard deviation [SD]; minimum [min]; maximum [max]) of adult female migratory caribou at calving and weaning. Data were collected from 2007 to 2009 on female-calf pairs from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, Northern Quebec and Labrador, Canada.

Body condition measurements	Calving								Weaning							
	RG				RAF				RG				RAF			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Total body mass (kg)	81.5	7.4	65.0	105.0	75.6	6.7	61.0	88.0	100.2	8.8	83.0	127.2	92.3	7.6	77.0	109.6
Dressed body mass (kg)	53.0	4.6	44.0	66.0	49.2	5.1	39.0	67.0	66.8	5.5	56.6	85.0	59.1	4.9	51.5	75.0
Total body length (cm)	182.4	8.4	166.0	205.0	178.6	8.2	152.0	195.0	184.9	7.7	171.0	199.0	179.6	9.2	158.0	199.0
Hind foot length (cm)	54.2	1.8	49.5	60.0	53.5	1.6	50.0	56.5	55.2	2.1	51.0	61.0	54.9	1.5	52.0	58.0
Chest girth (cm)	108.9	4.6	101.0	118.5	105.0	5.6	85.0	114.0	117.8	8.4	102.0	144.0	113.6	4.8	98.0	127.0
Femoral bone length (cm)	28.9	1.0	27.0	31.1	28.8	0.8	26.8	30.3	29.4	1.0	27.6	32.3	29.1	1.0	26.6	31.5
Mandible length (cm)	277.3	8.7	255.8	291.0	275.7	8.6	259.2	297.5	279.9	6.8	262.4	292.4	277.4	8.9	261.6	295.9
Peroneus muscle mass (g)	150.5	15.3	125.0	190.0	134.3	14.8	105.0	175.0	180.5	18.1	130.0	232.0	163.0	17.9	127.0	201.0
Kidney fat (%)	7.8	4.2	0.0	18.5	6.7	3.7	0.7	16.6	12.7	7.5	1.4	36.5	8.3	5.3	0.4	27.2
Femoral bone marrow fat (%)	63.1	16.4	20.1	90.1	62.1	15.3	23.7	87.3	84.2	6.1	58.8	93.1	74.9	12.4	36.7	89.0

TABLE III. PC scores (eigenvectors) from the PCA of body condition measurements of female-calf pairs of migratory caribou at calving and weaning, Rivière-George and Rivière-aux-Feuilles herds, Northern Quebec and Labrador, Canada. Numbers in bold identify body condition measurements with scores higher than 0.5 (see Jolliffe, 1986) for each PC axis retained.

Body condition measurements	Adult females					Calves	
	Calving		Weaning			Calving	Weaning
	PC1	PC2	PC1	PC2	PC3	PC1	PC1
Total body mass (kg)	0.88	0.24	0.58	0.40	0.52	0.95	0.92
Dressed body mass (kg)	0.86	0.28	0.65	0.39	0.54	-	0.92
Total body length (cm)	0.72	0.26	0.79	0.02	-0.18	-	0.68
Hind foot length (cm)	0.34	0.79	0.01	0.81	0.09	0.89	0.83
Chest girth (cm)	0.74	0.36	0.66	0.16	0.29	-	0.84
Femoral bone length (cm)	0.36	0.83	0.16	0.81	-0.11	-	-
Mandible length (cm)	0.27	0.81	0.43	0.63	-0.05	-	-
Peroneus muscle mass (g)	0.71	0.35	0.53	0.39	0.47	0.91	0.92
Kidney fat (%)	0.11	0.08	-0.11	-0.05	0.79	0.16	0.19
Femoral bone marrow fat (%)	0.09	0.01	0.23	-0.12	0.76	-	0.26

Calving



Weaning

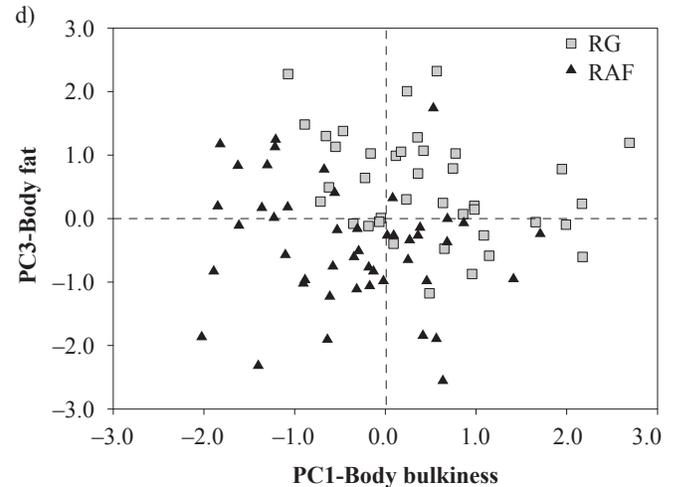
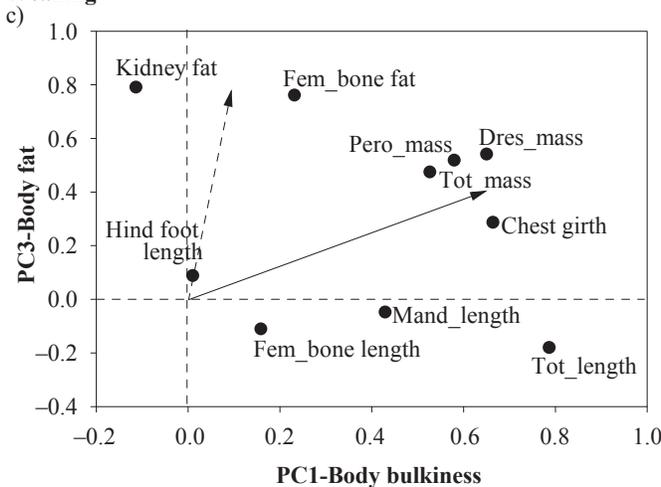


FIGURE 1. Principal component analyses (PCA) of body condition measurements of adult female migratory caribou at calving and weaning. Calving: a) body condition measurements selected by the first and second PC axes and b) scores of the first and second PC axes for both herds. Weaning: c) body condition measurements selected by the first and third PC axes and d) scores of the first and third PC axes for both herds. The following measurements were used in the PCAs: Total body mass (Tot_mass; kg), dressed body mass (Dres_mass; kg), total body length (Tot_length; cm), hind foot length (cm), chest girth (cm), femoral bone length (Fem_bone length; cm), mandible length (Mand_length; cm), peroneus muscle mass (Pero_mass; g), kidney fat (%) and femoral bone marrow fat (Fem_bone_fat; %). Data were collected from 2007 to 2009 on female-calf pairs from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, Northern Quebec and Labrador, Canada.

CALVES

For newborn calves, only 1 PC was retained (consecutive eigenvalues [% variation explained]: PC1: 2.75 [68.8%]). PC1 corresponded to a body mass/size index opposing heavy and tall calves with high protein reserves to light and short ones with low protein reserves (for body condition measurements, see Table IV, and for eigenvectors, see Table III). Kidney fat was not selected by the PCA (PC2: 0.85 [21.2%]).

At weaning, the first PC was retained (consecutive eigenvalues [% variation explained]: PC1: 5.27 [65.9%]). PC1 corresponded to a combination of body mass and size measurements opposing heavy and tall individuals with high protein reserves to light and short ones with low protein reserves (Table III and Table IV). Bone marrow fat (PC2: 0.95 [11.9%]) and kidney fat (PC3: 0.63 [7.9%]) were not selected by the PCA.

Discussion

We assessed body condition of migratory caribou female-calf pairs using multiple measurements of size, mass, and fat depth to identify which measurement(s) had the greatest influence on a composite measure of body condition at calving and weaning. Our results indicate that the body condition of adult females is best described by a body bulkiness index opposing heavy and long/round-bodied females to light and short/slender-bodied females at both calving and weaning. At weaning, however, adult females can also be differentiated by their fat reserves. Calf body condition is best described by body mass at birth and by a combination of mass and size measurements at weaning, opposing heavy and tall individuals with high protein reserves to light and short ones with low protein reserves. Overall, body mass appears to be the measurement that best describe individual variability in body condition of females and calves at calving and weaning.

At both calving and weaning, body mass, peroneus muscle mass, total body length, and chest girth were all related and together explained the highest percentage of inter-individual variability among measurements collected on adult females. This combination of measurements suggests that variations in female body condi-

tion are driven by variations in body mass and protein reserves (i.e., change in muscle mass) at both calving and weaning. For northern large ungulates, daily requirements in energy can increase by 20 to 40% during pregnancy (Chan-McLeod, White & Holleman, 1994), and parturition occurs when fat reserves are at their yearly minimum (Schwartz & Hundertmark, 1993). Protein reserves sustain fetal growth, particularly in late winter, when 80% of fetal mass is deposited (Pekins, Smith & Mautz, 1998; Chan-McLeod, White & Russell, 1999). As fat reserves are generally depleted in late spring, female body condition could be more affected by protein deficiency than by low fat reserves prior to calving (Huot, 1989; Parker, Barboza & Gillingham, 2009). Therefore, we suggest that measurements of body protein reserves, using indirect and non-invasive (body mass) or direct measurement (peroneus muscle mass), should be a priority at calving.

During summer, female ungulates face high energetic demands related to lactation (White & Luick, 1984; Therrien et al., 2007) that can increase daily requirements in energy and protein by 60–130% (Barboza & Parker, 2008). The energetic demands of lactation can reduce female body mass (red deer, *Cervus elaphus*, Mitchell, McCowan & Nicholson, 1976; white-tailed deer, *Odocoileus virginianus*, Simard et al., 2010), fat reserves (caribou, Chan-McLeod, White & Russell, 1999; white-tailed deer, Simard et al., 2010), and peroneus mass (white-tailed deer, Simard et al., 2010). During summer and fall, females replenish their body reserves and allocate energy to maintenance, future reproduction, and energy storage (Barboza, Parker & Hume, 2009). We observed that body fat measurements were grouped to explain variability in body condition of adult females in early fall, suggesting that females start building up fat reserves only following the physiological weaning of calves. Huot (1989) also observed limited fat accumulation in summer by female caribou, a possible consequence of high lactation requirements and poor summer habitat. A previous study also showed strong seasonal variability and an unusual increase in body fat deposition from fall to early spring for females of the Rivière-George herd (Couturier et al., 2009b). Couturier et al. (2009b) suggested that caribou could reach

TABLE IV. Body condition measurements (mean; standard deviation (SD); minimum (min); maximum (max)) of migratory caribou calves at calving and weaning. Data were collected from 2007 to 2009 on female-calf pairs from the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) herds, Northern Quebec and Labrador, Canada.

Body condition measurements	Calving								Weaning							
	RG				RAF				RG				RAF			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Total body mass (kg)	6.05	0.9	3.9	8.1	5.35	0.8	3.7	6.6	51.2	6.0	35.6	64.2	41.6	6.1	26.5	54.0
Dressed body mass (kg)	-	-	-	-	-	-	-	-	35.9	4.4	24.9	44.2	28.1	4.6	17.6	38.0
Total body length (cm)	75.9	6.3	64.0	86.2	74.1	5.3	65.0	84.0	146.2	6.8	126.0	161.0	139.1	7.8	120.0	156.0
Hind foot length (cm)	33.3	1.6	29.0	37.2	32.5	1.6	29.0	36.0	49.0	1.9	45.0	53.0	46.9	2.1	43.0	52.0
Chest girth (cm)	-	-	-	-	-	-	-	-	93.1	6.8	80.0	114.0	85.4	6.4	68.0	96.0
Femoral bone length (cm)	-	-	-	-	-	-	-	-	26.2	2.3	23.4	30.3	23.2	1.0	20.8	25.6
Mandible length (cm)	-	-	-	-	-	-	-	-	210.5	7.3	190.1	222.7	199.7	9.7	170.0	215.7
Peroneus muscle mass (g)	13.8	2.4	9.0	19.0	11.9	2.5	7.0	16.0	103.6	13.9	75.0	138.0	80.4	15.9	45.0	123.0
Kidney fat (%)	40.0	11.8	21.4	73.3	28.9	10.1	4.2	50.0	14.9	7.9	3.4	42.3	9.4	5.2	1.0	26.4
Femoral bone marrow fat (%)	-	-	-	-	-	-	-	-	81.2	8.7	47.4	96.3	74.4	11.7	36.8	89.8

a set point in protein deposition but not in fat reserves in the fall. We suggest that to assess body condition when using invasive sampling, it would be best to measure fat reserves from early fall to early spring and protein reserves from late spring to early fall. Percent body fat in early to mid-winter could therefore be an indicator of the subsequent probability of survival and reproduction (Parker, Barboza & Gillingham, 2009; Couturier *et al.*, 2009b). For several other northern ungulates, however, fat reserves are mainly deposited during summer (Cook, Cook & Mech, 2004; Parker, Barboza & Gillingham, 2009) or throughout fall (Simard *et al.*, 2010), influencing winter survival and reproduction (Parker, Barboza & Gillingham, 2009; Simard *et al.*, 2010).

Measurements commonly collected to assess body size of individuals include hind foot length, total body length, and chest girth (McElligott *et al.*, 2001; Cook, Cook & Irwin, 2003). Body size can provide information on condition during growth (Barboza, Parker & Hume, 2009), but it can also be related to reserves accumulation, as females with larger body size accumulate higher fat reserves compared to smaller females (Festa-Bianchet, Gaillard & Jorgenson, 1998). Our analysis indicates that total body length and chest girth explain similar inter-individual variability in body condition to body mass (Table III, Figure 1a–c). Chest girth and body length represent overall bulkiness and partly measure skeletal size but are highly affected by rumen fill (in the case of chest girth) and nutritional conditions through size-independent variation in body mass (Cook, Cook & Irwin, 2003; Simard *et al.*, 2010). In studies of red deer and reindeer, jaw and femur lengths have been used to monitor body size (Reimers, Klein & Sorumgard, 1983; Loison & Langvatn, 1998; Couturier *et al.*, 2010). In our study, hind foot length was associated with lengths of other bones (femur and mandible, Figure 1a–c), suggesting that it is a good index of skeletal size, as also suggested for other ungulates (McElligott *et al.*, 2001; Simard *et al.*, 2010). We suggest that the choice of measure of body size should depend on whether one is mainly interested in monitoring body bulkiness or skeletal size. Moreover, as noted above, chest girth can be influenced by rumen fill (Cook, Cook & Irwin, 2003), and thus this measure should be corrected when possible. Chest girth provides a good index of bulkiness, but hind foot length is a better estimator of body size.

As in adult females, the body mass and protein reserves (peroneus mass) of calves explained high percentages of inter-individual variability among measurements collected at both calving and weaning. Hind foot length at calving and hind foot length, total body length, and chest girth at weaning were also closely related to body mass and protein reserves. During early development, juvenile ungulates allocate metabolic resources in priority to body growth and then to fat accumulation (Barboza, Parker & Hume, 2009). They have higher rates of protein turnover and skeletal growth compared to adults (Barboza, Parker & Hume, 2009). In calves, changes in mass therefore integrate variations in body size, body shape, and protein reserves. As juveniles face trade-offs in allocating energy to growth,

maintenance, and energy storage, reaching a high body mass and body size in early life could influence short-term survival (Gaillard *et al.*, 1997) and possibly adult size (Forchhammer *et al.*, 2001; Gaillard *et al.*, 2003).

Our analyses revealed that body mass best describes individual variability in body condition of adult females and calves at both calving and weaning, a result supported by previous studies of ungulates (Hewison *et al.*, 1996; Lesage *et al.*, 2001; Gaillard *et al.*, 2003; Barboza, Parker & Hume, 2009; Parker, Barboza & Gillingham, 2009). Body mass was associated with several PC axes, suggesting that it is associated with a number of variables measured, such as body size, fat, or protein reserves, and integrates several body condition components. Body mass, therefore, should be collected in priority when assessing body condition of ungulates, as it integrates variation in protein and fat reserves, is relatively easy to measure in wild animals, and is widely used to describe seasonal variations in body condition (Parker, Barboza & Gillingham, 2009). Chest girth or total body length should only be measured when measures of body mass are not feasible due to field conditions (*e.g.*, with large animals). In these situations, chest girth or total body length should be calibrated and used as an alternative index of the overall bulkiness of individuals. Hind foot length, on live and dead animals, and mandible length (Couturier *et al.*, 2010) on dead animals should also be collected to estimate skeletal size. On dead animals, collection of peroneus muscles, or other muscle groups that correlate with protein reserves, should be collected to provide useful measurements of protein reserves. Finally, kidney fat, especially from early fall to late winter for caribou (Couturier *et al.*, 2009b), should be estimated to evaluate individual fat reserves.

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