

Brief Communication

Modeling energy and protein reserves in support of gestation and lactation: glucose as a limiting metabolite in caribou and reindeer

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Introduction

In the CARMA (CircumArctic *Rangifer* Monitoring and Assessment) network we account for factors that affect reproduction and growth of an individual caribou through an energy/protein model, which simulates body weight and condition of an individual female caribou (*Rangifer tarandus*) over time (Russell *et al.*, 2005; Gunn *et al.*, 2013; White *et al.*, 2013). However, modeling mobilization of maternal fat and protein to support fetal growth and lactation is complex because energy and protein transactions occur through intermediary substrates (*e.g.*, fatty acids, glucose, amino acids). In the energy/protein model, however, we do not overtly deal with intermediary substrates; rather, we model the amount of body fat and protein that can be measured in the field. CARMA has a large body condition data set for Arctic caribou (*Rangifer tarandus*) populations that allow us to set limits on seasonal fat

and protein mobilization and accretion rates. Within the model we estimate daily energy and protein balances, and if negative, we estimate the amount of fat and protein that needs to be mobilized to satisfy demands. During gestation this exercise controls fetal growth, and during lactation it controls milk production and calf growth. As validation we rely on seasonal changes in body composition of female caribou (*R. t. granti*) of the Porcupine caribou herd (PCH) (Gerhart *et al.*, 1996) and experimental data derived from caribou and reindeer (*R. t. tarandus*) fed a known diet and intake during late gestation (Barboza & Parker, 2006; 2008).

Defining labile fat and protein reserves

Body fat constitutes the major energy reserve in *Rangifer* (Reimers *et al.*, 1982; Adamczweski *et al.*, 1987; Gerhart *et al.*, 1996) and we have termed this the labile fat reserve (LFR). A labile protein reserve (LPR) is protein that is

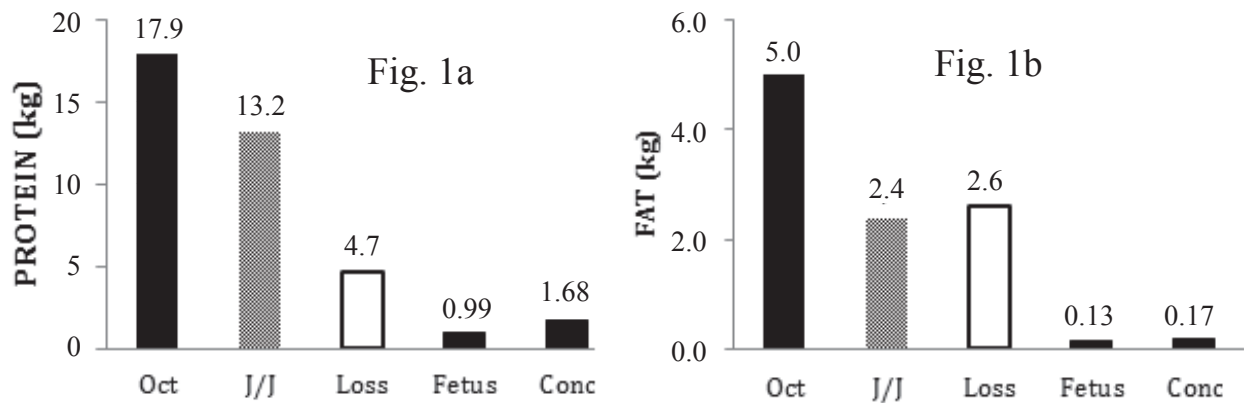


Fig. 1. Mean overwinter loss in body protein (a) and body fat (b) based on body composition measured on females of the Porcupine Herd in October (Oct) and June-July (J/J) (Gerhart *et al.*, 1996). The amount of fetal and conceptus (Conc.) protein (a) and fat (b) were made in the same females in J/J. Note the differences in scales for protein and fat.

mobilized over winter or early lactation. The LPR is difficult to define anatomically or at the tissue level; therefore we quantify it from seasonal changes in body composition. Studies on reindeer and caribou suggest that about 78% of mobilized protein is derived from skeletal muscle and 22% from the viscera (*e.g.*, liver, kidneys, alimentary tract; Reimers *et al.*, 1982; Gerhart *et al.*, 1996). Repeated measures of body composition calculated from estimates of body water using isotope studies (Cameron & Luick, 1972; Holleman *et al.*, 1982; Chan-McLeod *et al.*, 1994; Barboza & Parker, 2008) have import for use with live animals, and these studies on reindeer and caribou (Barboza & Parker, 2008; Parker *et al.*, 2005; 2009) challenge the assumption that the ability of ruminants to catabolize body protein is limited (Reid *et al.*, 1966; Nolan & Leng, 1968). Mobilized body protein as amino acids is used to satisfy gestation and lactation demands, and when oxidized, amino acids also are a source of energy. In the model, we only allow fat and protein to be mobilized down to lower limits ensuring that fat (F_m) and protein (P_m) are retained in sufficient amounts for life processes.

In the CARMA energy/protein model, we define F_m as 2-3% of body weight (Adamczewski *et al.*, 1987; Huot 1989; Gerhart *et al.*, 1996) and consider this to be a fat reserve defended

during gestation (FR_g) and lactation (FR_l). We set the P_m defended in gestation (PR_g) at 13 kg because this value approximates the minimum body protein required for conception (calculated from Gerhart *et al.*, 1997), and it approximates that for puberty in caribou. Several studies show the P_m during early lactation is lower than at calving by about 1 kg. Actual LPR and LFR vary annually and depend on the levels of body protein and fat of females entering winter. Fat reserves vary independent of protein among populations and are dependent on reproductive history of the female (Parker *et al.*, 2005, 2009). Although body protein is often thought to be only poorly mobilized, data from *Rangifer* populations would challenge this assumption since the seasonal change in body protein is about 26-42% (Huot 1989; Gerhart *et al.*, 1996; Chan-McLeod *et al.*, 1999) giving a LPR of 3-6 kg. The 4.6 kg protein loss (Fig. 1a) exceeds that for fat (2.6 kg, Fig. 1b).

Capture of mobilized reserves by the conceptus

Important to modeling gestation is determining the fractions of LFR and LPR that are captured by the conceptus (fetus plus tissues) in contrast to that used in metabolic processes. Based on data for the PCH we calculated that 36% of the LPR was retained by the conceptus (Fig. 2a), but only 6.5% of the LFR was

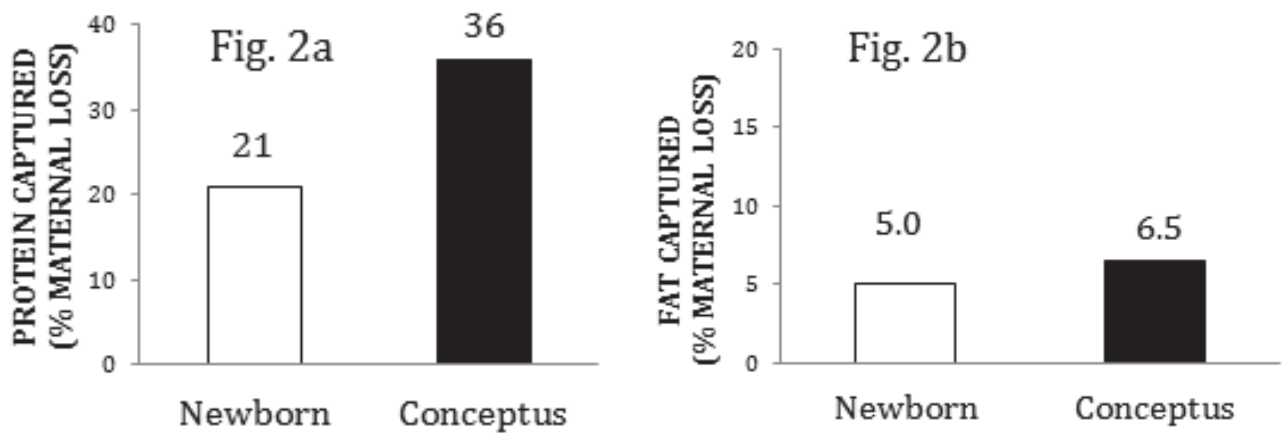


Fig. 2. Percent capture of protein (a) and fat (b) by the newborn fetus and conceptus of caribou of the Porcupine Herd based on the overwinter changes in body composition (Gerhart *et al.*, 1996). Note the differences in scales for protein and fat.

captured (Fig. 2b). The low capture rate for the LFR was expected given that body fat is a major metabolic reserve of the animal. These estimates represent the integral of the entire gestation period and are probably low compared with late gestation when fetal demands increase exponentially. Barboza & Parker (2008) report reindeer and caribou protein and fat balances in females and their offspring at near term and the third week of lactation. We converted their data to absolute values (Fig. 3). Daily, 42% of maternal protein loss (26 g) was captured by the fetus. Of the daily loss of fat, 15% (8.1 g)

was captured. Both data sets (Fig. 1, 3) indicate considerable protein-N and fat is not captured and these differences must be accounted for in the model. Although we do not model intermediary substrates in calculating energy and protein-N metabolism, we must include their fundamental processes within the energy-protein algorithms of the model. For the fetus, glucose but not fatty acids constitutes the source of energy for metabolism (Barcroft, 1946), and demand for glucose increases dramatically during the last trimester.

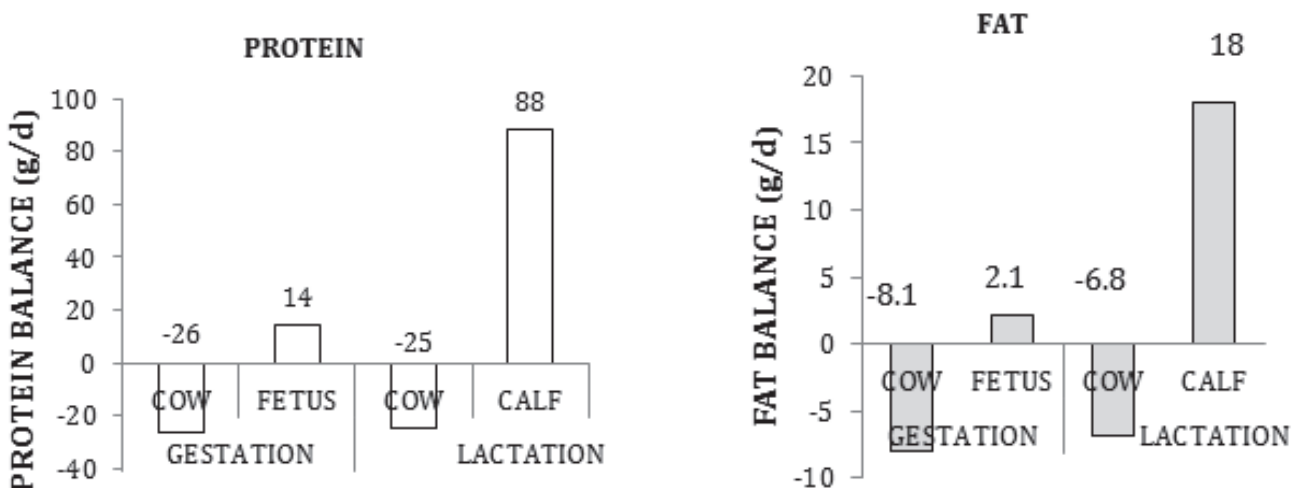


Fig. 3. Balance of protein (a) and fat (b) in caribou at term gestation and at three week lactation in relation to protein and fat deposition of the fetus and calf in caribou given diets of known composition. Calculations are based on data of Barboza & Parker (2008). Stable isotope analysis was used by Barboza and Parker to deduce the maternal versus dietary sources of protein and fat deposited in the offspring.

Table 1. Estimation of glucose synthesis by a caribou at term gestation based on isotope estimates of urea production. At 58 g/d this synthesis would require the metabolism of 105 g protein. Comparison is made with the likely demand for glucose by the fetus. An estimate made from the irreversible loss (IL) of glucose measured in near-term reindeer and caribou minus the glucose IL measured in non-pregnant animals fed at maintenance. A second estimate of fetal demand is calculated from the glucose uptake of the conceptus at term in sheep.

Body weight (kg)	Urea Entry Rate (g/d)	Possible Glucose Synthesis from Amino Acids (g/d)	Fetus Weight (kg)	Fetal Glucose Requirement (g/d)
105	36.8	57.7	6.4	83 ¹ -110 ²
Barboza & Parker, 2008	518 mgN/kg ^{0.75} .d and BW = 105 kg. Barboza & Parker, 2008	Gluconeogenesis from 100 g protein gives 55 g glucose and 35 g urea. Krebs, 1964	Barboza & Parker, 2008	

¹ 13 g/kg fetus per d based on glucose IL at term minus maintenance glucose IL (McEwan *et al.*, 1976).

² 17 g/kg fetus per d (Hodgson *et al.*, 1991).

Gluconeogenic demand

If glucose cannot be met by dietary precursors, it must be met mainly by gluconeogenesis from glucogenic amino acids of the LPR. Krebs (1964) has shown that gluconeogenesis from 100 g of protein results in the formation of 35 g urea (25.4 g urea-N) and 55 g glucose. Thus estimates of urea production can be used to estimate gluconeogenesis during pregnancy (Nolan & Leng, 1968). Barboza & Parker (2008) have made estimates of urea production, termed urea entry rate when isotopes are used. From their estimates we calculate that gluconeogenesis is 58 g glucose/d for this study (Table 1). Synthesis of 58 g glucose uses about 105 g of protein daily. Daily fetal glucose requirements vary from 83-110 g/d for a 6.4 kg fetus (Table 1), suggesting as much as 50% of fetal glucose requirements could be met by pro-

tein at terminal pregnancy.

During early lactation glucose is required for lactose synthesis. As an example, for an 85 kg caribou that produces daily about 1.2 L milk, 52 g lactose is synthesized. At higher rates of milk secretion, approaching 2 L/d, the supply of glucose precursors for lactose synthesis can limit lactose synthesis (White & Luick, 1976). In turn, the rate of lactose synthesis exerts a strong control over the level of milk production in ruminants (Annison *et al.*, 1968). Thus, whenever dietary glucose precursors cannot meet glucose demands the LPR is tapped. The minimum LPR, about 1 kg, could supply as much as 550 g glucose that could last for several days as a supplement to dietary precursors. However, this potential glucose supplement would be less because of the competing demand on body protein for synthesis of milk protein.

Important to modeling is accounting for the contribution made by dietary protein to protein deposition (NRC, 2007) and to glucose synthesis during gestation and lactation (McEwan *et al.*, 1976; White & Luick, 1976).

Adaptive and ecological influences over energy and protein reserves: work in progress

Interactions between energy and protein must account for animal responses (Chan-McLeod *et al.*, 1994) and for nutrition as a fundamental integrator of *Rangifer* responses to the environment (Parker *et al.*, 2009). Given that reindeer express a greater dependency on body reserves than do caribou in late gestation and early lactation (Barboza & Parker, 2006), the question as to whether caribou and reindeer respond with similarly evolved responses to the use of body reserves relative to resource availability remains to be studied. We assumed the relative

use of reserves for the same resource availability would be the same for both subspecies. Finally, the modeling process needs to reflect interacting components of ecological drivers (Russell *et al.*, 1993) while preserving our ability to analyze the implications for intermediary metabolism. Temporal and spatial aspects of phenological and biomass changes on calving grounds of caribou and reindeer that are reported as responses to climate change are complex, but nevertheless phenological mismatches are proposed (Post *et al.*, 2009). A thorough analysis of these environmental effects on intake and reproduction in relation to body reserves is warranted (Gunn *et al.*, 2009; Griffith *et al.*, 2010) given the fundamental role of meeting glucose requirements as we have detailed above.

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