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Regulation of rumen fermentation during seasonal fluctuations in food intake of muskoxen

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Abstract

We studied rumen fermentation of castrated adult muskoxen (*Ovibos moschatus*; $n=4$) during periods of low (May) and high (August) food intake. Turnover time (17±1.8 h) and volume (26±3.9 L) of rumen fluid were consistent between May and August and among days within each season. Rumen temperature did not vary significantly during the day (38.8±0.29 °C) in either season. Rumen osmolality (271.9±16.4 vs. 245.9±11.4 mOsm kg^{-1}) and pH (6.81±0.31 vs. 6.39±0.15) were higher in May than in August indicating a shift in the allostatic set point. Rumen fluid pH was more variable in May than in August both before and after a single meal of fermentable substrate even though fermentation acids were lower in May than in August (101.0±11.0 vs. 126.0±8.74 mM). Changing proportions of minor fermentation acids indicated a shift in metabolic pathways even though bacterial numbers were similar between seasons (6.4±5.8×10^9 mL^{-1}). Allostatic set points probably alter the homeostatic range of conditions and the microbial diversity of fermentations in herbivores from highly seasonal environments.

Keywords: Arctic; Bacteria; Digesta passage; Homeostasis; Hyperphagia; Rumen; Short chain fatty acids; Winter

1. Introduction

Animals that rely on digestive fermentation for their principle source of energy must maintain stable conditions of temperature, osmolality, and acidity for their microbial symbionts (Hungate, 1966). Foregut fermentations such as the rumen are more vulnerable to fluctuations in the physical and chemical properties of food and water than fermentation systems in the lower tract (Stevens and Hume, 1995). Rumen microorganisms handle a wide variety of fermentative substrates from toxins to structural carbohydrates, proteins, and starches. Large imbalances in substrate load, such as excess starch, can force the rumen microbial ecosystem into disequilibrium resulting in excess production of gas, fermentation acids, and even death of the host (Russell and Rychlik, 2001; Owens et al., 1998). The rumen is a complex of mutualistic relationships not only between the host and its microbes, but also amongst the microbial phylotypes (Hungate, 1966; Stahl et al., 1988). Digestive fermentation is, therefore, an outcome of multiple routes of metabolism with cascading pools of substrate and product. Rumen microbes are reliant upon the substrates consumed as food by the host. The host also mixes the substrates and the microbes, triturates solid substrates, and maintains temperature, osmolality and acid balance that serve the microbial population (Russell, 2002). Natural shifts in food intake alter substrate availability to the microbes and impose a greater burden for services from the host. The rumen may be considered an allostatic system (Sterling and Eyer, 1988) where changes in food selection and intake by the animal shift conditions to new set points. Each meal may be considered a short-term load of substrate that tests the homeostatic response to acute shifts in rumen conditions.

Muskoxen are grazing ruminants (*Ovibos moschatus*) from highly seasonal arctic habitats where food abundance and composition changes widely throughout the year (Staaland and

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Table 1
Mean composition of dry matter in hay and supplement fed to cannulated muskoxen during May (hypophagia) and August (hyperphagia)

Component (g DMg^{-1})	Hay		Supplement	
	May	August	May	August
Dry matter	0.96	0.96	0.98	0.97
NDF	0.62	0.67	0.30	0.33
Hemicellulose	0.30	0.31	0.15	0.18
ADF	0.32	0.35	0.15	0.15
Cellulose	0.29	0.32	0.13	0.13
Lignin	0.03	0.03	0.02	0.02
Ash	0.04	0.07	0.08	0.09

Variation within samples was less than 5% (CV).

Thing, 1991; Blix, 2005). Ruminal fermentation accounts for 80% of cellulose degradation in muskoxen (Barboza et al., 2006). Substrate loads for rumen microbes can increase with food intakes of muskoxen by 74% from spring (hypophagia) to autumn (hyperphagia; Barboza et al., 2006). Unstable or variable conditions within the rumen may be associated with reductions in the number and activity of bacteria in muskoxen during winter (Barboza et al., 2006). Declines in rumen pH accompany seasonal hyperphagia as well as the consumption of fermentable supplements by muskoxen (Barboza et al., 2006). Concentrations of short chain fatty acids (SCFA) produced from fermentation increase in concert with seasonal food intake in muskoxen (Barboza et al., 2006). Concomitant changes in the pattern of SCFA concentration also suggest small shifts in substrate degradation pathways. Patterns of SCFA infer diversity of substrate and probably the expression of pathways by novel enzymes and/or novel microorganisms.

We tested the general hypothesis that ruminal conditions change with season in muskoxen. Food intakes are typically low (hypophagia) from January to June but increase (hyperphagia) from August through October as body mass is gained (Peltier et al., 2003). We predicted a shift in both the allostatic set point and the variability around that set point between May (hypophagia) and August (hyperphagia). The ruminal environment was characterized by measuring diurnal fluctuations in temperature, pH, and osmolality during May and August. We tested the effect of substrate load in each period by providing muskoxen with an acute load of fermentable material as part of their normal supplement of minerals. Concomitant changes in rumen volume and fluid outflow were measured with two external markers (Co-EDTA; Cr-EDTA) in each period. The effect of substrate load on microbial dynamics was assessed by direct counts of the number of rumen bacteria and the concentrations of SCFA during each season.

2. Materials and methods

2.1. Animals

Muskoxen (*O. moschatus*) were studied at the R. G. White Large Animal Research Station (Fairbanks, AK; 65N, 146W) under protocol #03–21 of the Institutional Animal Care and Use Committee, University of Alaska, Fairbanks. We used 4 castrated adult muskoxen (6.4 to 9.5 years) that were surgically cannulated at the rumen 3 years prior to the experiment. Animals were housed in a large pen (2043 m^2) with water and hay (*Bromus* sp.) provided ad libitum. A pelleted mineral supplement (M-Ration, Alaska Pet and Garden, Anchorage, Alaska) was provided twice each week at 17.5 $g \cdot kg^{-0.75}$ body mass. The supplement consisted of starches and soluble proteins from cereal grains that are more rapidly degraded in the rumen than grass hay (Barboza et al., 2006). Body mass was routinely recorded (±0.5 kg; model 703 scale, Tru-Test, San Antonio, Texas) during handling and averaged for each month from 2002–2005 to describe two annual cycles.

2.2. Food and digesta composition

Hay and supplement were collected each week during May and August to measure food composition (Table 1). Food samples were dried for 48 h at 50 °C to determine dry matter content. Dried foods were ground to pass through a 2 mm screen in a Wiley mill (Arthur Thompson Company, Philadelphia, Pennsylvania) for further analyses. Milled feeds were dried to constant mass at 80 °C to determine analytical dry matter. Ash content was measured by combusting 1 g of dried material for 8 h at 500 °C in a muffle furnace (Barnstead International, Dubuque, Iowa). Fiber extractions followed the procedures of Peltier et al. (2003) and were performed sequentially as follows: neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin. Content of hemicellulose was determined as the difference between NDF and ADF whereas content of cellulose was determined as the difference between ADF and lignin (Van Soest et al., 1991; Peltier et al., 2003).

2.3. Fluid markers

We used two solute markers (cobalt and chromium ethylenediaminetetraacetic acid, Co-EDTA and Cr-EDTA) to measure rumen volume and turnover time on two subsequent days during spring and autumn. Co-EDTA and Cr-EDTA were

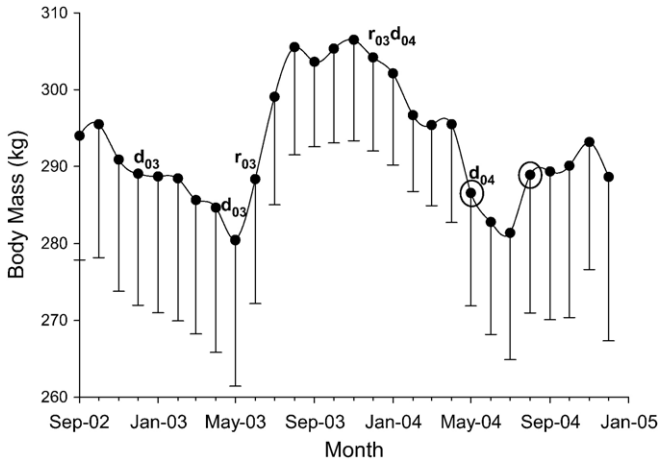

Fig. 1. Body mass (kg) of castrated muskoxen ($n=4$; mean−SD) fed grass hay ad libitum from 2002 through 2004. Circles correspond to study periods in May and August 2004. Letters indicate significant differences in body mass ($P<0.05$) associated with seasonal declines (d) and rises (r) in each year (03 or 04).