Could a big gut be too costly for muskoxen (Ovibos moschatus) in their first winter?

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Abstract

Young mammalian herbivores are more vulnerable to harsh winter conditions than adults, especially among large circumpolar species like the muskox (Ovibos moschatus). We compared feeding responses of muskox calves (body mass 95 kg) with those of mature, non-reproductive females (body mass 227 kg) in mid-winter when air temperatures fell to −40 °C. Food intakes (1.8−2.2 kg digestible dry matter (DM) d−1), digesta fill (27−32 kg wet mass) and digestibility of hay (52−58% of DM; 49−55% of gross energy) were similar between age groups even though calves were much smaller than adults. Calves fed more frequently (12 vs. 8 feeding bouts per day) and thus spent more time feeding each day than adults (387 vs. 343 min per day). High mass-specific food intakes of calves indicate higher requirements for maintenance of body tissue than adults, which could be related to a larger intestinal tract in young muskoxen. Notably, cows and calves maintained a constant body mass throughout, indicating that they were feeding at maintenance levels and that the relatively higher intakes of calves were not related to growth. Together, these data suggest that limited food availability due to snow cover or high animal density may reduce the survival of muskoxen in their first winter.

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

1   Could a big gut be too costly for muskoxen (*Ovibos moschatus*) in their first winter?

2

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12

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14   capacity

15

1

2 **Abstract**

3 Young mammalian herbivores are more vulnerable to harsh winter conditions than adults,

4 especially among large circumpolar species like the muskox (*Ovibos moschatus*). We

5 compared feeding responses of muskox calves (body mass 95 kg) with those of mature,

6 non-reproductive females (body mass 227 kg) in mid-winter when air temperatures fell to

7 -40°C. Food intakes (1.8 to 2.2 kg digestible dry-matter d^{-1}), digesta fill (27 to 32 kg wet

8 mass) and digestibility of hay (52 to 58% of dry matter; 49 to 55 % of gross energy) were

9 similar between age groups even though calves were much smaller than adults. Calves

10 fed more frequently (12 vs. 8 feeding bouts per day) and thus spent more time feeding

11 each day than adults (387 vs. 343 min per day). High mass-specific food intakes of calves

12 indicate higher requirements for maintenance of body tissue than adults, which could be

13 related to a larger intestinal tract in young muskoxen. Notably, cows and calves

14 maintained a constant body mass throughout, indicating that they were feeding at

15 maintenance levels and that the relatively higher intakes of calves were not related to

16 growth. Together, these data suggest that limited food availability due to snow cover or

17 high animal density may reduce the survival of muskoxen in their first winter.

18

1 **Introduction**

2 The population dynamics of large herbivores are often dominated by the survival of

3 juveniles through their first year of life (Gaillard et al., 1998). This phenomenon has been

4 observed for numerous species, among ungulates (Gaillard et al., 2000), and also among

5 kangaroos (Bayliss, 1985; Dawson, 1995). Juvenile mortality is influenced by four

6 factors: disease, predation, environmental exposure and nutrition. Risks of predation and

7 disease are highest for neonates and decline progressively with age. Juveniles are also

8 most vulnerable to adverse conditions, such as prolonged drought (e.g. kangaroos in

9 Australia; Bayliss, 1985; Robertson, 1986) or severe winters (e.g. red deer in Norway,

10 Loison and Langvatn, 1998; elk in North America, Garrott et al., 2003). Nutrition

11 contributes to all three factors because lack of sufficient energy stores (body fat), low

12 food abundance, poor food quality, and digestive constraints (e.g. limited gut capacity

13 and/or digestive efficiency) debilitate juveniles and increase their vulnerability to other

14 causes of mortality.

15 Muskoxen (*Ovibos moschatus*) are large (> 200 kg) ruminants whose population

16 biology is heavily influenced by calf survival (Thing et al., 1987; Aastrup and Mosbech,

17 2000; Reynolds et al., 2002). Juvenile muskoxen face extreme winters with ambient

18 temperatures (T_a) that are frequently below -40°C, and as low as -80°C with wind chill

19 (Blix, 2005). The principal foods of muskoxen are grasses and sedges, which are low in

20 both abundance and quality in winter (Klein and Bay, 1991; Ihl and Klein, 2001; Larter

21 and Nagy, 2001). Muskoxen calve shortly before spring, which allows the young to

22 continue growing when forage availability and quality are highest in autumn (Reynolds et

23 al., 2002). Newborn muskoxen weigh 6-8 kg and are well equipped to deal with the

1 challenging thermal environment. In addition to being extremely well insulated, neonates

2 use brown fat for non-shivering thermogenesis (Blix et al., 1984) in the first few weeks

3 postpartum (Adamczewski et al., 1995), as do most large mammals (Alexander, 1979).

4 Young muskoxen continue to grow rapidly through spring and summer and by the onset

5 of winter in October they are normally around 70-80 kg body mass, or around 1/3 the size

6 of adults (200-250 kg) (Knott et al., 2004; Peltier and Barboza, 2003). By this stage,

7 calves are normally weaned, though lactation can extend through winter depending on the

8 body condition and nutritional status of calf and mother (Adamczewski et al., 1998;

9 White et al., 1987; White et al., 1989; Parker et al., 1990).

10   Winter mortality of muskox calves has been associated with prolonged and severe

11 cold, particularly when combined with wind, and deep or hard-packed snow

12 (Forchhammer and Boertmann, 1993; Reynolds et al., 2002). A small body size could

13 impact directly on their costs for thermoregulation. Small animals have higher surface

14 area to volume ratios and generally lose heat more readily than larger animals with

15 similar insulation. Moreover, muskoxen calves enter their first winter carrying less body

16 fat than adults (Adamczewski et al., 1995; Peltier and Barboza, 2003), providing them

17 with less tissue insulation against low T_as and fewer energy reserves to combat food

18 shortages (Larter and Nagy, 2001).

19   For herbivores like muskoxen, body size is particularly important because of the

20 time required for fermentative digestion. Small herbivores usually have smaller absolute

21 gut sizes and faster rates of food passage, which can limit microbial action on forage and

22 reduce digestive efficiency (Demment and Van Soest, 1985; Robbins, 1993), although

23 this view has recently been challenged by Clauss et al. (2007). Nonetheless, smaller

1   herbivores are usually less able to exploit fibrous, low-quality diets (Demment and Van

2   Soest, 1985; Cork, 1994), such as those available to muskoxen in winter (Klein and Bay,

3   1991; Ihl and Klein, 2001; Larter and Nagy, 2001; Reynolds et al., 2002). Additionally,

4   with shorter legs and lower chest heights, muskox calves may struggle with increased

5   locomotor costs in deep snow, or they may have higher costs associated with digging

6   through hard-packed ice crusts to access the forage below (Fancy and White, 1985;

7   Forchhammer and Boertmann, 1993; Ihl and Klein, 2001).

8   In this study we compared the feeding patterns and forage digestion for captive

9   juvenile and adult muskoxen during mid-winter. We controlled several important factors

10   that confound field observations: food quality and accessibility of food, disease and

11   predation. By removing these confounding factors, we were able to directly compare

12   nutritional responses of muskox calves with mature, non-reproductive cows under the

13   same environmental conditions. We experienced two extremes of winter conditions

14   during the study, a relatively warm week (T_a ca. -5°C) and a cold week (T_a ca. -30°C),

15   which allowed us to compare cow and calf feeding patterns and digestion in relation to

16   their thermal environment.

17

18   **Materials and Methods**

19   *Animals*

20   Muskoxen were studied at the University of Alaska Fairbanks, R.G. White Large Animal

21   Research Station (LARS; Fairbanks Alaska; lat 65°N, long 146°W). Animals were

22   studied through mid-winter, between December 20th 2004 and January 24th 2005. Mature

23   female (Cows; n = 6) were not pregnant, at least 10 years old (mean ± SEM = 13.4 ± 0.8)

1   and had a mean (± SEM) body mass of 227.5 ± 2.4 kg at the beginning of the study.

2   Calves (n = 3; 2 male, 1 female) were born between April 8th and May 17th 2004. At the

3   beginning of the study the mean (± SEM) calf age was 7.8 ± 0.4 months, and they had

4   mean (± SEM) body mass of 95.2 ± 5.0 kg. Individual cows and calves were identified

5   using reflective ribbon (2 cm x 50 cm) braided into a small patch of fur.

6   Calves were separated from their mothers and weaned on December 1st 2004. The

7   mothers of those calves were not used in this experiment. Thereafter the calves were held

8   together in one pen (0.2 ha) that was directly adjacent to the pen (0.5 ha) for cows. Snow

9   (water) and long (unchopped) Brome grass hay (*Bromus* sp.; Table 1) was provided ad

10   libitum. All animals were fed a daily ration of a supplement containing milled grain and

11   alfalfa with minerals and vitamins (Alaska Pet and Garden, Anchorage Alaska; Table 1).

12   Cows and calves consumed 200 g and 100 g air-dry mass d^{-1} of pelleted supplement

13   respectively, which was equivalent to 3.0 g dry matter $kg^{-0.75} d^{-1}$ for both groups. The

14   pellet rations were always completely consumed. All animals were trained to regular

15   handling and restraint using a squeeze chute that was housed in a large barn. Animals

16   were herded through the barn and chute daily between 0800 h and 0900 h, weighed (± 0.5

17   kg; Tru-Test Model 703 scale; San Antonio, Texas) and fed the ration of pellets.

18

19   *Weather*

20   We recorded ambient temperature (T_a), wind speed, wind gust speed and solar radiation

21   every 10 min (HOBO Weather Station, Bourne, Massachusetts). Wind speeds and T_a

22   were measured at the height of adult female muskoxen (110 cm). Snowfall was recorded

23   3 km south of LARS at the Agricultural & Forestry Experiment Station.

1

2 *Animal Behaviour and Feeding Patterns*

3 Behavioural observations of captive muskoxen were carried out in two 5-day bouts in

4 early January 2005. The first bout (WEEK 1) commenced at 0900 h on January 3 and was

5 terminated on January 8 at 0800 h. The second bout (WEEK 2) commenced at 0900 h on

6 January 9 and was terminated on January 14 at 0800 h. Thus, during WEEK 1 and

7 WEEK 2 animals were observed continuously for 23 h d^{-1}. Observations were not

8 recorded between 0800 and 0900 h daily as the animals were disturbed for collection of

9 faeces, body mass weighing and other procedures (see below).

10 Animals were observed from a tower (height 4.3 m) overlooking both pens. Hay

11 was provided in a feeder that was located within 15 m from the base of the tower. Fresh

12 hay was offered at irregular times each day to prevent entrainment of feeding patterns.

13 When there was sufficient daylight animals were easily observed and identified by the

14 naked eye or by using binoculars. Under low light conditions, animals were identified

15 using a hand-held night-vision scope (Infra-red Imager, Rostov Cyclops 8M, Russia). We

16 used a point-sampling technique (Dunbar 1976) for the quantitative recording of specific

17 behaviours, including lying, feeding, standing without feeding, moving (walking or

18 running), playing and other (e.g. eating snow, scratching). Play behaviour was recorded

19 as interactions such as head shaking, head butting and body pushing that were observed

20 away from the feeder. Total activity was calculated as the sum of time spent on all

21 recorded events excluding lying. Point sampling scans were made every 10 minutes. The

22 times of initiation and termination of each feeding bout was recorded for each animal to

23 calculate total feeding time.

1 *Faecal Output and Hay Digestibility*

2 Faecal output was estimated in WEEK 1 and WEEK 2 by continuous dosing with an

3 indigestible marker, Chromium (Cr), fed to each animal as Chromium oxide (Cr_2O_3;

4 Brandyberry et al., 1991; see also Musimba et al., 1987). The Cr_2O_3 marker was packed

5 into gelatine capsules (Gel-cap, Size #0, 0.68 mL; Torpac New Jersey) to $\pm$ 0.01 g. The

6 Cr_2O_3 was fed to each animal daily between 0800 h and 0900 h by mixing capsules with

7 their daily pellet ration. Doses for Cr_2O_3 were 1.0 g and 0.75 g d^{-1} (i.e. 0.7 g and 0.5 g Cr)

8 for the cows and calves respectively. We dosed animals each day for 14 days before the

9 experiment (WEEK 1) to equilibrate the contents of the digestive tract with Cr_2O_3.

10 Dosing continued for a further 15 d throughout the observation period. Fresh faecal

11 samples (ca. 100 – 200 g wet-mass) were collected before dosing each morning and

12 frozen for subsequent analysis. Faecal dry matter (DM) output by each animal was

13 calculated from the concentration of indigestible Cr in the faeces according to

14 Brandyberry et al., (1991):

15
$$\text{Faecal output (g DM d}^{-1}) = \frac{\text{Cr dose (mg d}^{-1})}{\text{Faecal Cr (mg g}^{-1}\text{ DM)}} \qquad (1).$$

16 Dietary Cr (Table 1) provided less than 0.001% of the daily marker dose for either cows

17 or calves.

18   Apparent DM and gross energy digestibility from the grass hay were estimated

19 using the naturally occurring micronutrient manganese (Mn). Absorption and secretion of

20 Mn in the gut of vertebrates is negligible and it has been used as a digestibility marker for

21 numerous species (e.g. Kaufman et al., 1976; Dawson et al., 1994; Rosen and Trites,

22 2000). Digestibility was estimated according to (Barboza et al., 2006):

1 $$\text{Apparent digestibility (\%)} = \left(1 - \frac{M_\text{d}/C_\text{d}}{M_\text{f}/C_\text{f}}\right) \cdot 100 \qquad (2);$$

2 where M_d = concentration of Mn in the hay diet; C_d = concentration of component (DM

3 or energy) in the hay diet; M_f = concentration of Mn faeces; and C_f = concentration of

4 component (DM or energy) in faeces. The pelleted ration did contain a quantity of Mn

5 that was excreted in faeces along with that from hay. Daily intakes of Mn from the

6 pelleted ration amounted to 14.8 mg and 7.4 mg for the cows and calves respectively.

7 This represented a constant influx of Mn and, assuming that it was 100% indigestible,

8 daily faecal Mn (g d^{-1}) outputs were corrected for each animal by subtracting 14.8 or 7.4

9 mg as appropriate. This provided an estimate of the faecal Mn that was eliminated solely

10 from the hay, which was then used to calculate apparent DM and energy digestibility.

11
12
13 *Dry Matter and Energy Intake*
14
15 Daily dry matter intake (DMI) and gross energy intake (EI) from grass hay were

16 estimated from the apparent digestibility and total faecal output of each component

17 according to:

18 $$\text{Intake} = \text{Faecal output}/(1 - \text{apparent digestibility}) \qquad (3);$$

19 where intakes and faecal outputs were g DM d^{-1} or kJ d^{-1}, and apparent digestibility is

20 fraction of intake. Apparent DM and energy digestibility were then to estimate digestible

21 dry matter intakes (DDMI) and digestible energy intakes (DEI) respectively.

22

1   *Rates of Food Passage and Mean Retention Time*

2   At the end of WEEK 2, the passage (ROP) of fluid and particulate markers through the

3   entire gastrointestinal tract was measured over 5 days. Passage of solutes was measured

4   using a pulse dose of cobalt-ethylenedinitrilotetraacetic acid (Co-EDTA) (Udén et al.,

5   1980). Doses were 2.0 g and 1.5 g Co-EDTA for cows and calves respectively. Doses

6   were administered using gelatine capsules (Gel-cap, Size #00 for cows and #0 for calves,

7   Torpac New Jersey), which are known to dissolve in water within a few minutes.

8   Capsules ($\pm$ 0.01 g Co-EDTA) were offered to animals along with their pelleted ration.

9   All animals ingested the markers within 5 min, except two cows that consumed the entire

10 dose over 40 min, but this did not appear to affect the appearance of the fluid marker in

11 their faeces- see results). One cow refused the Co-EDTA. Thus, passage of the fluid

12 marker was measured in n = 5 cows and n = 3 calves.

13   The passage of particulates was measured using ytterbium (Yb) mordanted to

14 plant cell walls as a marker and offered in a pulse dose (Udén et al., 1980). Cell walls

15 (neutral-detergent fibre) were prepared by neutral detergent washing (Van Soest et al.,

16 1991) of previously collected muskoxen faeces dried at 50°C for 48 h and coarsely

17 ground (Barboza et al., 2006). After neutral-detergent washing, faecal fibre was separated

18 into size classes by wet sieving and particles between 500 μm and 1000 μm were retained

19 for mordanting (Udén et al., 1980). The Yb-mordant was packed into gelatine capsules ($\pm$

20 0.01g; Gel-cap, Size # 000, 1.37 mL; Torpac New Jersey) and offered to animals along

21 with their pellet ration. Doses of the Yb-mordant were 3.2 g for adults (8 capsules) and

22 1.6 g for calves (4 capsules). Only three animals (two calves and one adult) ingested the

23 entire dose in capsule form. In all other cases, the dose was mixed directly with the pellet

1   ration and as such actual doses were unknown. Even when mixed with a pellet ration, n =

2   3 cows refused the dose. Thus, passage of the particulate marker was measured in n = 3

3   cows and n = 3 calves.

4   After dosing, all animals were released to their respective pens and fresh faecal

5   samples were collected directly from the ice/snow at approximately 4, 8, 12, 24, 48, 72,

6   96 and 120 h post dose. Samples were immediately stored frozen for later analysis (see

7   below *Sample Preparation and Analysis)*. Mean retention times (MRT) of each marker

8   were calculated according to Thielemans et al. (1978; see also Warner, 1981):

9
$$\text{MRT (h)} = \frac{\sum(C_i T_i \Delta T_i)}{\sum C_i \Delta T_i} \qquad (4);$$

10   where C_i is the concentration of marker (Co or Yb) in faeces collected at the *i*th

11   defecation post dose at time T_i and ΔT_i is the interval between subsequent samples.

12

13   *Gastrointestinal Tract Fills*

14   Total DM in digesta (i.e. dry gut fill) for cows (n = 3) and calves (n = 3) was calculated

15   from the MRT of particulate marker, the average faecal output and the average DM

16   digestibility (Holleman and White, 1989). Indigestible fill (V_N; g DM) was calculated as:

17
$$V_N = F \bullet \text{MRT} \qquad (5);$$

18   where F = faecal output (g DM h^{-1}) and MRT = particle MRT (h). Total digestive tract

19   fill (V; g DM), was then calculated as the sum of the indigestible and digestible fill

20   according to:

21
$$V = V_N + \frac{V_N \bullet A}{2(1-A)} \qquad (6);$$

1 where A = fractional apparent DM digestibility and assuming that the absorption of

2 ingested food occurs linearly (see Holleman and White, 1989). It should be noted that the

3 marked particles used to measure particle MRT may not have represented the full range

4 of digesta particle sizes, but our results provide a useful index of total DM digesta

5 contents (see also Gross et al., 1996). Total wet-matter contents of the entire

6 gastrointestinal tract were then estimated assuming digesta moisture was 88% (after

7 Knott et al., 2004).

8

9 *Sample Preparation and Chemical Analysis*

10 Food and faeces were dried in a forced convection oven at 55°C (Robertson and Van

11 Soest, 1981) until constant mass. Dry faeces were bulked separately for WEEK 1 and

12 WEEK 2 for each animal by randomly selecting 5 pellets from each day's collection. Dry

13 feed (hay and pellets) and bulked faeces were then ground through a 1.25 mm mesh (#20)

14 using a Wiley Mill (Arthur Thomas Co., Scientific Apparatus, Philadelphia, USA) before

15 analysis for gross energy and mineral contents (Cr, Mn, Co and Yb). Energy contents

16 were determined in duplicate by combusting sub-samples (0.7 g) in an adiabatic bomb

17 calorimeter (Parr Instruments, Boleen, IL.). Mineral contents of hay, pellet ration and

18 bulked faeces (WEEK 1 and WEEK 2) were determined by directly coupled plasma

19 spectrometry (DCP; Peltier et al., 2003).

20

1 *Statistical analysis*

2 All statistical tests were performed using Minitab for Windows 12.1 (1998; Minitab Inc.,

3 PA, USA) and JMP for windows (JMP 5.1.2 SAS Institute Inc, NC). Means are reported

4 ± 1 standard error (SEM).

5 We used repeated measures general linearised models (GLM) to compare specific

6 behaviours as proportion of all recorded behavioural events within and between weeks.

7 Proportional data were arcsine transformed prior to analysis. Other behaviours, including

8 feeding time, number of feeding bouts and bout length, were also analysed using repeated

9 measures GLMs with animal (i.e. subject) as a random factor. Play (%) was compared

10 within and between weeks using Friedman's tests, a non-parametric ANOVA for

11 repeated measures (Zar, 1999). Significant differences detected by Friedman's test were

12 further investigated using equation 11.3 from Zar (1999) with standard error adjusted for

13 repeated measures and critical $q = 0.05$ (Zar, 1999).

14 We used repeated measures GLMs to compare body mass, faecal output (DM and

15 energy), apparent digestibility (DM and energy) and whole animal feed intake (DMI,

16 DDMI, EI and DEI) within and between ages from WEEK 1 and WEEK 2, with animal

17 (subject) as a random factor. Digestibilities were arcsine transformed prior to analysis.

18 The MRTs for the digesta markers (Co and Cr) were compared within age classes using

19 paired 2-tailed t-tests, and between ages using unpaired 2-tailed t-tests. At the beginning

20 of WEEK 2, one calf refused further Cr_2O_3 doses and its faecal output for WEEK 2 was

21 estimated as a missing data point according to Snedecor and Cochran (1989) for a

22 randomised block design (Hume, 1974).

1   The small sample size for calves when combined with a repeated measures design

2   did not provide sufficient degrees of freedom for an analysis of co-variance to examine

3   body size effects on intakes (dry matter or energy). Consequently, we compared intakes

4   (DMI, DDMI, EI and DEI) by cows and calves within and between weeks on an

5   allometric basis. For this we used a body mass exponent of 0.75 (Kleiber, 1975; Schmidt-

6   Nielsen, 1984; Hayssen and Lacy, 1985; Nagy et al., 1999).

7   　　　Assumptions for statistical analysis were tested using the Kolmogorov-Smirnov

8   test for normality ($\alpha = 0.05$) and Levene's test for homogeneity of variances ($\alpha = 0.05$).

9   To account for violation of normality or homogeneity of variances, allometrically-

10   adjusted DDMIs (g kg$^{-0.75}$ d^{-1}g), energy intakes (kJ kg$^{-0.75}$ d^{-1}) and DEIs (kJ kg$^{-0.75}$ d^{-1}) for

11   cows and calves were log$_{10}$ transformed prior to analysis. There were no significant

12   interactions between animal age and week for any response variable.

13

14   **Results**

15   *Weather*

16   Ambient conditions during the study are summarized in Table 2. Average ambient

17   temperature dropped by 28°C from WEEK 1, a relatively "warm" period, to WEEK 2,

18   which we defined as a "cold" period. The ensuing period for measures of rate of passage

19   was 8°C warmer than WEEK 2. Wind and solar radiation were low throughout the study

20   (Table 2). Snow fell only during WEEK 1 for a total accumulation of 28.5 cm between

21   days 1 and 4.

22

Feeding Patterns and Other Behaviour

Feeding bouts (min) were similar between age classes, but bouts were 5-10% longer in the cold week (WEEK 2) than in the warm week (WEEK 1) for both age groups (Table 3). Consequently, total amount of time spent feeding was increased by 22 min d^{-1} for cows and by 30 min d^{-1} for calves between the warm week (WEEK 1) and the cold week (WEEK 2; Table 3; $P < 0.05$). Calves had an average of four additional feeding bouts each day compared with cows in both WEEK 1 and WEEK 2. Calves spent more time feeding than the cows in WEEK 1 and WEEK 2 by 34.3 min d^{-1} and 44.7 min d^{-1}, respectively (Table 3; $P < 0.05$).

Differences in the feeding patterns of cows and calves were reflected in their time budgets. Calves spent also more time feeding than cows when examined as a proportion of all recorded behaviours (Table 4). The proportions of time spent feeding by cows and calves were also greater in WEEK 2 than in WEEK 1 (Table 4). When not feeding, cows and calves spent the bulk of their time lying; this comprised 60-70% of all recorded behaviours. On average, cows spent more time lying than calves in both weeks (Table 4). All other behaviours such as moving, standing and playing each comprised 5% or less of all recorded observations (Table 4). The calves did exhibit play behaviours that were not observed for the cows in either week (Table 4). There were no significant differences in the proportion of time spent playing by calves between WEEK 1 and WEEK 2 ($P > 0.05$; Table 4). The proportion of time active did not differ between the warm and cold weeks for each age group (Table 4).

1   *Faecal Output and Forage Digestibility*

2   Faecal Cr concentrations reached a plateau in cows and calves by the commencement of

3   WEEK 1; the average concentration of Cr from bulked daily faecal samples for all

4   muskoxen was 381 ± 18 μg g^{-1} DM for WEEK 1. Faecal DM (kg d^{-1}) or energy (MJ d^{-1})

5   outputs were not significantly different between cows and calves in either WEEK 1 or

6   WEEK 2. There were also no significant differences in faecal DM or energy outputs

7   within each age class between weeks (Table 5). There were no significant differences

8   between cow and calf apparent digestibilities for DM or energy from the grass hay diet

9   (Table 5). However, the apparent digestibility of DM from hay was significantly lower in

10 WEEK 2 compared with WEEK 1 for both the cows and calves, by around 4-5 percent (*P*

11 = 0.05; Table 5).

12

13 *Dry Matter and Energy Intakes*

14 Calves consumed as much gross DM and digestible DM as cows in both the warm

15 (WEEK 1) and the cold (WEEK 2) weeks (Table 5). There were no significant

16 differences within each age class between weeks for either gross DMI or DDMI.

17 Similarly, we found no significant differences in whole-animal gross energy intakes or

18 DEIs between age classes in either WEEK 1 or WEEK 2, and no significant differences

19 between weeks within ages (Table 5). On an allomteric basis, DDMI and DEIs by calves

20 (kg$^{-0.75}$ body mass d^{-1}) were 1.8-1.9 times greater than those of the cows (*P* < 0.001; Table

21 6).

1   *Feed Passage and Mean Retention Time*

2   Patterns of elimination for both fluid (Co) and particulate (Yb) markers from cows and

3   calves were similar, but passage rates were generally faster among calves (Fig. 1). Cows

4   retained markers (i.e. MRTs) longer than calves; 13 h longer for fluids and 6 h longer for

5   particles (Table 7). Within each age class, retention of the fluid marker was shorter than

6   that of marked particles (Yb), by around 10 h for cows and 15 h for calves (Table 7).

7

8   -------Insert Fig. 1 near here------

9

10 *Gastrointestinal Fill*

11 Absolute fill (kg) of digesta in the gastrointestinal tract was similar between cows and

12 calves for both wet and dry mass (Table 8). However, per unit of body mass the ingesta

13 (dry and wet) content of calves was twice that of cows ($P < 0.01$). On an allometric basis

14 (i.e. per $kg^{0.75}$), calves digesta content was 1.6 times greater than that of cows ($P < 0.01$;

15 Table 8).

16

17 **Discussion**

18 Seasonal activity and movement of free-ranging muskoxen are lowest in mid-winter

19 compared with other seasons. Wild animals usually travel less than 1.0 km d^{-1} and spend

20 the greater portion of their time lying (resting, sheltering or ruminating; Forchhammer,

21 1995; Reynolds et al., 2002). Similarly, in our captive study, cows and calves spent the

22 greater portion of their day lying (ca. 70%), with little activity other than feeding (ca. 23-

23 30%). However, our captive muskoxen spent half as much time feeding (5.3-6.5 h d^{-1};

1   Table 3) as comparably aged free-ranging animals during mid-winter (10-12 h d^{-1};

2   Forchhammer, 1995). Animals in the field therefore spend more time, and presumably

3   more energy, on feeding. Additional costs would include movement within and between

4   feed patches and also that for digging through ice-crusts to access forage. More

5   importantly, we found that calves spent more time feeding than did cows, and they

6   required more daily feeding bouts (Table 3) to achieve the same levels of feed intake (kg

7   DM d^{-1}; Table 5).

8   The smaller body size of the muskox calves could influence their feed intakes via

9   several paths. A small body size is usually associated with faster rates of food passage

10   (Robbins, 1993), which is particularly important for herbivores because it may limit the

11   time available for microbial fermentation. Whether such generalisations apply to

12   juveniles within species is uncertain, but recent analyses have argued that MRT is less

13   affected by body size in adult herbivores than was previously thought, both between and

14   within species (Clauss et al., 2006; Clauss et al., 2007). Nonetheless, food passage for

15   both fluid and particulate markers was faster for our muskoxen calves compared with

16   cows (Table 7). Whether this difference was less than expected given their 3-fold

17   difference in body mass is difficult to say. More information on the intraspecific scaling

18   of gut size, feed intake and body mass for muskoxen is required and particularly using

19   animals across the full range of ages and sexes.

20   The MRTs for both fluid and particle markers for our muskox cows were

21   comparable to those previously reported for castrated males fed grass hay in mid-winter

22   (ca. 44 h for fluids and 49 h for particles; Barboza et al., 2006). Consequently, forage

23   digestibility might be expected to be lower for the muskoxen calves compared with

1   adults, but that was not the case here. We found that the apparent digestibility of DM

2   from brome hay was similar for cows and calves within both the warm and cold week

3   trials (range 52-58%; Table 5), and was comparable to that reported for castrated males

4   fed brome hay in mid-winter (ca. 50%; Peltier et al., 2003). Interestingly, DM

5   digestibility by cows and calves was slightly lower in the cold week than the warm week

6   (Table 5). Ingestion of cold food may reduce fermentation rate in muskoxen even though

7   their ruminal microbes are apparently tolerant of cold shocks (Crater and Barboza, 2007).

8   Regardless, the relatively higher feed intakes and greater number of feeding bouts by

9   calves were not related to a lesser ability to digest the grass hay diet.

10   Passage of digesta is less variable than digesta fill in muskoxen. Seasonal

11   increases in food intake of adults by 74% is associated with an increase in rumen turnover

12   of only 10%, but a gain in digesta fill of 58% (Barboza et al., 2006). Retention in the

13   intestines is much longer and more variable than in the rumen for muskoxen.

14   Consequently, high food intakes and digesta fill of calves in winter may be associated

15   with a greater role for post-ruminal digestion and colonic fermentation in calves than in

16   adults. Lichen consumption in winter has been associated with an increase in post-

17   ruminal fermentation in reindeer (White et al., 1984; Sormo et al., 1999). However, an

18   absolutely smaller rumen could constrain the amount of food calves can ingest during a

19   single feeding bout; rumen size (empty wet tissue mass) per unit body mass in 60-day old

20   muskox calves was comparable to that of adults (Knott et al., 2004). In other words,

21   rumen fill and overall processing capacity, rather than digestibility of forage, may dictate

22   feed intake patterns of calves in mid-winter.

1   The levels of wet-ingesta fill for the muskoxen cows in this study were somewhat

2   lower than those previously reported for wild cows. In our study, wet-ingesta were

3   around 14% body mass, compared with 25% for wild cows (Adamczewski et al., 1995).

4   The animals in Adamczewski et al.'s (1995) study, however, were collected feeding on

5   natural diets outside of winter, and both forage quality and season can affect ingesta loads

6   (Barboza et al., 2006). These data suggest that our captive females possessed reserve gut-

7   capacity in mid-winter. Adult herbivores in other species have been shown to posses

8   reserve gut capacity when nutritional demands are minimal (e.g. non-reproductive ibex;

9   Gross et al., 1996) or when food quality is high (e.g. non-reproductive kangaroos; Munn

10   and Dawson, 2006). Food intake of pregnant muskoxen is probably the same as that of

11   non-pregnant females. Pregnancy does not affect food intakes of caribou in winter

12   (Parker et al., 2005), and most of the demands of pregnancy are met by body fat and

13   protein in caribou and reindeer (Barboza and Parker, 2006; Barboza and Parker, 2007)

14   and also in muskoxen (Rombach et al., 2002). However, an apparent "spare capacity" in

15   reproductive females could support higher food intakes for lactation during late winter

16   and early spring (Jenks et al., 1994). Muskoxen can also increase winter gut-fluid

17   volumes to autumnal levels at low ambient temperatures, indicating that they can use

18   their reserve capacity as conditions demand (Crater et al., 2007). Our muskox calves, on

19   the other hand, did not appear to possess similar reserve gut-capacity. Wet-ingesta

20   contents of the calves were ca. 28% body mass, comparable to that of wild juveniles in

21   autumn (ca. 25% body mass; Adamczewski et al., 1995) when feed intakes and growth

22   rates are highest (Peltier et al., 2003; Knott et al., 2005). This would suggest that the

1   calves in our study were feeding at or near the maximum capacity of the digestive tract,

2   which is similar to reports for other young herbivores (Munn and Dawson 2006).

3   On an allomteric basis, gross DM and gross energy intakes by the cows in our

4   study were comparable to those previously reported for mature, free ranging

5   (Forchhammer, 1995) and captive, non-pregnant (Adamczewski et al., 1994) cows in late

6   winter. Notably, the calves in our study had the same DMI and DDMI as cows that were

7   more than double their body mass (Table 5). Thus, on an allometric basis (i.e. kJ kg$^{-0.75}$ d^{-}

8   ^{1}) calves ingested 1.8-1.9 times as much digestible DM and digestible energy as adults

9   (Table 6). In general, high DEIs of juvenile mammals compared with adults are usually

10   attributed to the additional costs of growth (Brody, 1945). But muskox calves routinely

11   stop growing through mid-winter (Peltier and Barboza, 2003), as was the case here,

12   making their relatively higher intakes somewhat perplexing. The calves must have

13   experienced higher energy costs, relative to adults, via some pathway other than growth.

14   Additional energy costs for thermoregulation are one possible explanation.

15   During winter, muskoxen can face temperature gradients between the

16   environment (T_a) and the body core in excess of 70°C (Blix, 2005). For calves, their

17   higher surface area to volume ratio could impact their daily energy budgets, particularly

18   in light of their more numerous foraging bouts and concomitant exposure to prevailing

19   conditions. However, if calves experienced relatively higher thermal costs then they

20   might have been expected to increase energy intakes more so than cows as T_a's declined,

21   but that was not the case here. At T_as as low as -40°C (WEEK 2), gross and digestible

22   energy intakes (MJ d^{-1}) by calves and cows were not significantly different (Table 5).

23   More importantly, DEIs by either cows or calves were not significantly higher in the

1 colder week than in the warmer week (Table 5). Given the exceptional protection offered

2 by muskoxen's winter underwool, or qiviut (Rowell et al., 2001), it is not surprising that

3 the T_as seen here may not have overly challenged our animals. Other northern ungulates

4 are known to have lower critical temperatures of -20°C (e.g. bighorn sheep; Chappel and

5 Hudson, 1978) and even -40°C (e.g. Svalbard reindeer; Nilssen et al., 1984), but the

6 thermoneutral range has never been measured for adult muskoxen.

7   Alternative to higher costs for thermoregulation, muskoxen calves may need to

8 support higher activity levels. Juveniles spent 6% more time on activities than adults,

9 which was mainly allocated to play behaviours (Table 4). Rates of energy demand (kJ

10 min^{-1}) for play interactions such as head butting were probably greater than the average

11 rate of expenditure for all other activities. Small differences in activity budgets may

12 therefore contribute to the higher energy intake of calves, but still cannot explain the

13 large difference in allometrically adjusted DEIs between age groups (kJ $kg^{-0.75}$ d^{-1})

14 (Table 6).

15   Overall, the higher DEIs by muskox calves in our study could not be completely

16 explained by extra demands for growth, thermal costs or activity, and are therefore

17 suggestive of intrinsically higher maintenance (and/or basal) energy requirements (MER)

18 compared with adults; MERs being the level of intake needed simply to maintain body

19 mass under thermoneutral conditions (Robbins, 1993). Although our animals may not

20 have been at thermoneutrality, all animals maintained body mass throughout (Table 5)

21 and consequently their energy intakes are reflective of winter MERs. Why calves might

22 have higher intrinsically energy requirements compared with adults is unclear, but our

23 data suggest it may be related to a relatively large gut system, at least in part.

1   Among adult herbivores gastrointestinal size (capacity) usually scales

2 isometrically with body mass (i.e. per kg^1; Demment and Van Soest, 1985). However, the

3 calves in our study had wet- and dry-ingesta loads that were approximately twice that of

4 the mature cows (kg kg^{-1} body mass; Table 7), suggestive of a relatively larger gut system

5 overall. Knott et al. (2004) found total gastrointestinal tissue (g kg^{-1}) in young muskoxen

6 (age 60 days) was 1.8 times that of adults. This was largely explained by the calf small

7 intestine being 4.8 times heavier (g kg^{-1}) than that of adults. Although 60-day calves

8 ingest significant forage by this stage, a larger small intestine is probably related to milk

9 consumption and utilization. That muskox calves can prolong weaning until after their

10 first winter (Adamczewski et al., 1998; White et al., 1989; Parker et al., 1990), suggests

11 that they may retain a relatively long small intestine through winter. The herbivore gut,

12 however, is arguably the most expensive organ system (Stevens and Hume, 1995) and

13 maintaining such a large gut may be decisively costly for young muskoxen during their

14 first winter.

15

16 **Conclusions**

17 Like many large herbivore species worldwide, muskoxen are a culturally and

18 economically important for local communities (Gunn, 1995). Predicting how large

19 herbivores might respond to a changing climate is especially difficult (e.g. Coulsen et al.,

20 2005) because there is insufficient information about the ecological physiology of

21 juveniles for most species. Here we have shown that even without the additional costs or

22 risks associated with free-living, there were fundamental differences in the relative

23 energy intakes and feeding patterns of juvenile and adult muskoxen in mid-winter. We

suggest that juvenile muskoxen may face a trade-off between having a large mass of
intestine to support rapid growth and fat build-up during the spring/autumn (Baldwin et
al., 2004; Knott et al., 2005), but they may be energetically constrained to supporting this
during their first winter, when forage is limited (Klein and Bay, 1991; Ihl and Klein,
2001; Larter and Nagy, 2001) but when suckling and thus milk intake is still possible
(Parker et al. 1990; White et al., 1997).

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14

1 **Acknowledgements**

10

11 **Figure Legends**

12 Figure 1: Elimination of A) fluid (Co) and B) particulate (Yb) markers in faeces ($\mu g\ g^{-1}$

13 DM) from mature female and young-of-the-year muskoxen fed Brome hay ad libitum in

14 mid-winter. (Note: for (A) n = 5 cows and n = 3 calves; and for (B) n = 3 cows and n = 3

15 calves).

16

17

Table 1

Table 1: Dry matter (DM), energy and minerals composition (mean ± SEM) of grass hay (*Bromus* sp.) and pellet supplement offered to muskoxen in mid-winter Alaska.

	Grass hay	Pellets
Dry matter (g 100 g^{-1} wet-mass)	83.7 ± 0.4	88.7 ± 0.01
Energy (kJ g^{-1} DM)	18.4 ± 0.01	17.4 ± 0.02
Cobalt (µg g^{-1} DM)	Trace (< 0.1)	0.2 ± 0.2
Manganese (µg g^{-1} DM)	62.1 ± 3.2	83.4 ± 2.5
Chromium (µg g^{-1} DM)	Trace (< 0.1)	3.4 ± 0.4

Table 2

Table 2: Weather conditions during WEEK 1, WEEK 2 and the food passage trial.

	WEEK 1 (n = 5 days)	WEEK 2 (n = 5 days)	Passage trial (n = 5 days)
Ambient temperature (°C)			
Average (± SEM)	-4.3 ± 0.1	-32.2 ± 0.3	-24.3 ± 0.1
Maximum	-0.3	-13.8	-16.2
Minimum	-10.2	-41.1	-28.1
Median	-4.4	-34.2	-25.3
Wind speed (km h^{-1})			
Average (± SEM)	1.5 ± 0.1	0.1 ± 0.0	0.02 ± 0.01
Maximum	15.1	4.1	2.7
Minimum	0.0	0.0	0.0
Median	0.0	0.0	0.0
Wind gust speed (km h^{-1})			
Average (± SEM)	7.0 ± 0.4	1.4 ± 0.1	1.5 ± 0.1
Maximum	46.6	13.7	9.6
Minimum	0.0	0.0	0.0
Median	2.7	0.0	1.4
Solar radiation (Watts m^{-2})			
Average (± SEM)	1.1 ± 0.1	4.2 ± 0.3	7.1 ± 0.7
Maximum	16.9	56.9	106.9
Minimum	0.6	0.6	0.6
Median	0.6	0.6	0.6

Table 3

Table 3: Feeding behaviour of mature female (Cow; n = 6) and young-of-the-year (Calf; n = 3) muskoxen during a warm (WEEK 1) and a cold (WEEK 2) week in mid-winter Alaska.

		WEEK 1	WEEK 2	Age Effect P-value
Feeding bouts (d^{-1})				
	Cow	8 ± 0.3^A	8 ± 0.5^A	$P < 0.01$
	Calf	12 ± 0.2^A	12 ± 0.4^A	
Bout length (min bout^{-1})				
	Cow	32.1 ± 3.0^A	35.5 ± 2.9^B	NS
	Calf	26.8 ± 1.5^A	28.0 ± 1.8^B	
Total feeding time (min d^{-1})				
	Cow	319.9 ± 15.6^A	342.6 ± 13.1^B	$P < 0.05$
	Calf	354.2 ± 4.7^A	387.3 ± 13.8^B	

Results are mean (± SEM); Means with different superscript letters denote significant differences between WEEK within age groups, a-b P ≤ 0.05.

Table 4

Table 4: Specific behaviours as a proportion (%) of all recorded behaviours for mature female (Cow; n = 6) and young-of-the-year (Calf; n = 3) muskoxen during a "warm" (WEEK 1) and a "cold" (WEEK 2) week in mid-winter Alaska.

		WEEK 1	WEEK 2	Age Effect P-value
Feeding (%)				
	Cow	22.8 ± 1.4^A	25.5 ± 0.6^B	$P < 0.05$
	Calf	25.6 ± 0.6^A	30.1 ± 1.9^B	
Lying (%)				
	Cow	70.2 ± 1.6^A	68.0 ± 0.9^A	$P < 0.001$
	Calf	63.4 ± 0.3^A	60.4 ± 2.5^A	
Moving (%)				
	Cow	0.9 ± 1.2^A	1.2 ± 0.3^A	NS
	Calf	1.6 ± 0.4^A	1.0 ± 0.2^A	
Standing (%)				
	Cow	5.1 ± 0.4^A	4.4 ± 0.3^A	NS
	Calf	3.5 ± 0.2^A	4.3 ± 0.6^A	
Playing (%)				
	Cow	0.02 ± 0.02^A	0.2 ± 0.1^A	$P < 0.001$
	Calf	4.3 ± 0.6^A	2.9 ± 0.4^A	
Other (%)				
	Cow	1.0 ± 0.3^A	0.7 ± 0.1^A	$P < 0.05$
	Calf	1.7 ± 0.3^A	1.3 ± 0.3^A	
Active (%)				
	Cow	29.8 ± 1.6^A	32.0 ± 0.9^A	$P < 0.001$
	Calf	36.6 ± 0.3^A	39.6 ± 2.5^A	

Results are means (± SEM); Letters denote significant differences between WEEK within age groups, a-b $P \le 0.05$.

Table 5

Table 5: Body mass (kg), whole-animal faecal outputs, apparent digestibility and intakes of grass hay (*Bromus* sp.) by mature female (Cow; n = 6) and young-of-the-year (Calf; n = 3) muskoxen during a "warm" (WEEK 1) and a "cold" (WEEK 2) week in mid-winter Alaska. (DM = Dry matter; DMI = Dry matter intake; DDMI = Digestible DMI; DEI = Digestible energy intake)

		WEEK 1	WEEK 2	Age Effect P-value
Body mass (kg)				
	Cow	228.7 ± 2.3^A	227.4 ± 2.4^A	$P < 0.001$
	Calf	95.5 ± 5.2^A	95.9 ± 5.2^A	
Faeces (kg DM d^{-1})				
	Cow	1.7 ± 0.9^A	1.7 ± 0.6^A	NS
	Calf	1.6 ± 1.6^A	1.5 ± 1.6^A	
Faecal energy (MJ d^{-1})				
	Cow	33.2 ± 1.8^A	33.7 ± 1.2^A	NS
	Calf	31.1 ± 3.3^A	29.2 ± 3.1^A	
Apparent DM digestibility (%)				
	Cow	56.1 ± 1.9^A	51.8 ± 1.1^B	NS
	Calf	58.1 ± 0.9^A	53.4 ± 3.5^B	
Apparent energy digestibility (%)				
	Cow	53.0 ± 2.1^A	48.8 ± 1.2^A	NS
	Calf	55.4 ± 0.9^A	50.7 ± 3.6^A	
[†]DMI (kg d^{-1})				
	Cow	3.9 ± 0.3^A (4.1)	3.6 ± 0.1^A (3.8)	NS

	Calf	3.8 ± 0.4^{A} (3.9)	3.3 ± 0.4^{A} (3.3)	
[†]DDMI (kg d^{-1})				
	Cow	2.2 ± 0.2^{A} (2.4)	1.9 ± 0.8^{A} (2.1)	NS
	Calf	2.1 ± 0.2^{A} (2.2)	1.8 ± 0.3^{A} (1.9)	
[†]Gross Energy intake (MJ d^{-1})				
	Cow	71.7 ± 5.6^{A} (75.2)	65.8 ± 2.2^{A} (69.3)	NS
	Calf	69.6 ± 6.9^{A} (71.3)	59.7 ± 7.3^{A} (61.4)	
[†]DEI (MJ d^{-1})				
	Cow	38.5 ± 4.1^{A} (41.1)	32.2 ± 1.4^{A} (34.8)	NS
	Calf	38.5 ± 3.8^{A} (39.8)	30.5 ± 5.1^{A} (31.8)	

Results are mean ($\pm$ SEM); Letters denote significant differences between WEEK within age groups, a-b $P \leq 0.05$; [†]Values in parenthesis are means including component intake (DM or energy) from the pelleted supplement, and assuming digestibility of DM and energy of pellets were comparable at 76% (Barboza, et al. 2006; see text).

Table 6

Table 6: Allometrically-adjusted (per $kg^{0.75}$) feed intakes by mature female (Cow; n = 6) and young-of-the-year (Calf; n = 3) muskoxen fed grass hay (*Bromus* sp.) during a "warm" (WEEK 1) and a "cold" (WEEK 2) week in mid-winter Alaska. (DMI = Dry matter intake; DDMI = Digestible DMI; DEI = Digestible energy intake)

		WEEK 1	WEEK 2	Age Effect *P*-value
[†]DMI (g $kg^{-0.75}$ d^{-1})				
	Cow	66.2 ± 4.8^{A} (69.2)	61.1 ± 2.0^{A} (64.1)	*P* < 0.001
	Calf	122.9 ± 8.7^{A} (125.8)	106.1 ± 12.5^{A} (109.0)	
[†]DDMI (g $kg^{-0.75}$ d^{-1})				
	Cow	37.6 ± 3.6^{A} (39.9)	31.7 ± 1.4^{A} (34.0)	*P* < 0.001
	Calf	71.4 ± 5.4^{A} (73.7)	57.3 ± 9.5^{A} (59.6)	
[†]Gross Energy intake (kJ $kg^{-0.75}$ d^{-1})				
	Cow	1218 ± 89^{A} (1269)	1124 ± 37^{A} (1175)	*P* < 0.001
	Calf	2261 ± 160^{A} (2312)	1950 ± 227^{A} (2001)	
[†]DEI (kJ $kg^{-0.75}$ d^{-1})				
	Cow	654 ± 66^{A} (693)	549 ± 25^{A} (588)	*P* < 0.001
	Calf	1253 ± 93^{A} (1292)	999 ± 168^{A} (1038)	

Results are mean (± SEM); Letters denote significant differences between WEEK within age groups, a-b $P \leq 0.05$; [†]Values in parenthesis are means including component intake (DM or energy) from the pelleted supplement, and assuming digestibility of DM and energy of pellets were comparable at 76% (Barboza et al., 2006; see text).

Table 7

Table 7: Mean retention times (MRT; h) for solute (Co) and particle (Yb) markers after a pulse dose in mature female (Cow) and young-of-the-year (Calf) muskoxen.

MRT (h)

	Solute (Co)	Particle (Yb)
Cow	39.4 ± 0.7^{A} (n = 5)	48.3 ± 0.9^{B} (n = 3)
Calf	27.6 ± 0.7^{A} (n = 3)	42.7 ± 1.4^{B} (n = 3)
Age Effect P-value	$P < 0.01$	$P < 0.05$

Results are mean ($\pm$ SEM); Letters denote significant differences between digesta markers (Co *vs* Yb) within age groups, a-b $P < 0.01$.

Table 8

Table 8: Estimated gastrointestinal tract fill (gut fill) of dry and wet ingesta for mature

female (Cow) and young-of-the-year (Calf) muskoxen fed brome hay ad libitum.

	Dry ingesta			Wet ingesta		
	(kg)	(g kg^{-1})	(g kg$^{-0.75}$)	(kg)	(g kg^{-1})	(g kg$^{-0.75}$)
Cow (n = 3)	3.7 ± 0.3	16.2 ± 0.8	62.9 ± 3.1	32.3 ± 1.9	142.2 ± 6.6	551.8 ± 28
Calf (n = 3)	3.1 ± 0.3	32.1 ± 2.6	100.4 ± 8.5	27.1 ± 2.8	281.4 ± 23	880.7 ± 74
Age Effect P-value	NS	$P < 0.01$	$P < 0.01$	NS	$P < 0.01$	$P < 0.01$

Results are mean ($\pm$ SEM).