

GROWTH IN ARCTIC UNGULATES: POSTNATAL DEVELOPMENT AND ORGAN MATURATION IN *RANGIFER TARANDUS* AND *OVIBOS MOSCHATUS*

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Young arctic ungulates must grow quickly to use forages available during brief summers. We measured growth and organ maturation in *Rangifer tarandus* (reindeer, caribou) and *Ovibos moschatus* (muskoxen) at 3 stages: the neonatal period (1–30 days), during transition from milk to plants (30–60 days), and at maturity. Although reindeer provided greater maternal investment than muskoxen in utero (6.9% compared with 4.8% maternal mass), both species grew at similar rates (0.002 compared with 0.005 day⁻¹). High thyroid secretion and large hepatic lipid reserves in neonates indicated high rates of energy metabolism for thermogenesis and use of nutrients sequestered in utero. Mass gains during the neonatal period were associated with large gastric abomasas that would allow young ungulates to digest milk soon after birth. Body growth continued during transition to forage (60 days of age), which was accompanied by expansion of rumen, small intestine, and colon. Growth and organ maturation of arctic ungulates, therefore, emphasizes maternal investment in utero and the duration of growth, with little variation in growth rate during both neonatal and transitional phases.

Key words: allometry, digestive morphology, gut, herbivore, life history, lipid, liver, ruminant, thyroid

Plasticity of growth and morphology allows animals to adapt to fluctuations in their environment and can modify the evolution of species (West-Eberhard 2003). The Arctic is a variable environment with large annual cycles of temperature, photoperiod, and plant availability (Pielou 1994). Arctic ungulates, such as *Rangifer tarandus* (reindeer, *R. t. tarandus*; caribou, *R. t. grantii*) and *Ovibos moschatus* (muskoxen), time reproduction, birth, and growth to coincide with increased photoperiod and plant availability during brief summers (Suttie and Webster 1995). Although studies have investigated the importance of habitat and quality of plants in relation to the mother through development of fetus and milk supply (Crete and Huot 1993; Rachlow and Bowyer 1994, 1998; White et al. 1997), few papers have examined how the quality of diet can affect growth and development in offspring. Limited quality and quantity of forage plants can constrain growth in young arctic ungulates (McEwan 1968; Olesen et al. 1991; Reimers et al. 1983). If growth is plastic among ruminants, arctic ungulates would be predicted to mature more rapidly than

species from temperate regions where the season for plant growth is longer. Furthermore, species such as reindeer and caribou that mature earlier (18 months in captivity—Chan-McLeod et al. 1994) would also grow faster than muskoxen that reproduce at an older age in the same arctic climate (>2 years in captivity—White et al. 1998).

Timing and synchrony of parturition in ungulates is a critical life-history characteristic that holds implications for survival of neonates (Bowyer 1991, 1998; Keech et al. 2000; Rachlow and Bowyer 1991). Reindeer and muskoxen are born in mid-April to early May (Adamczewski et al. 1997; White and Luick 1984) before the peak in plant growth, whereas caribou are born in June near the time of plant emergence (Gerhart et al. 1996; Griffith et al. 2002). Young arctic ungulates use energy from milk and plants for growth during their 1st summer but grow slowly or lose muscle and fat during the 1st winter (Adamczewski et al. 1987; Eastland et al. 1989; Peltier and Barboza 2003). Adequate nutrition during development, therefore, is essential to meet high demands of growth during the first summer and to establish reserves before winter.

Although neonatal ruminants are well-developed somatically, young must expand the capacity and function of visceral systems and digestive tract to transition from milk to forage diets (Batt 1980; Janssens and Ternouth 1987; Lyford 1988; Owens et al. 1993). Young reindeer, caribou, and muskoxen have

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similar intakes of highly concentrated milk after birth, but time-to-weaning may be greater in muskoxen (8 months) than reindeer (5 months—Parker et al. 1990). Transition from milk to plants increases the load of structural carbohydrates that require fermentative degradation in the rumen (Van Soest 1994). Maturation of nutritional organs, such as the digestive tract, liver, and kidneys, also includes enlargement of viscera to reach the functional morphology of adults and support of greater food intakes (Lyford 1988). Morphological development of nutritional organs may also relate to greater consumption of fibrous plants in muskoxen than in reindeer and caribou (Hofmann 2000; Ihl and Klein 2001; Klein and Bay 1990; Staalnd et al. 1995). Because early phenologies of plants hold the greatest nutritional value and are the most digestible (Johnstone et al. 2002; Jorgenson et al. 2002), organ maturation of young ungulates must also coincide with growth of plants in the Arctic and precede senescence of those plants as forage quality declines into winter.

Arctic ungulates likely respond to environmental fluctuations through endogenous signals that integrate cues of photoperiod and temperature with systemic changes in growth and metabolism. Elevated concentration of thyroid hormones (T4 and T3) have been associated with increases in feed intake, body mass, antler development, and mating in ruminants at high latitudes (Loudon et al. 1989; Shi and Barrell 1992). Thyroid hormones may promote similar metabolic responses to the demands for rapid growth in the Arctic (Ryg and Jacobson 1982).

In this study, we compared growth of the somatic and visceral components of muskoxen with reindeer and caribou in the neonatal period (1–30 days), during the transition to forage consumption (30–60 days), and at maturity. We measured the mass and composition of organs, as well as the concentrations of thyroid hormones, to assess functional changes in morphology and endocrine correlates of metabolism. Changes in viscera were compared with the ingested diet and with growth of the whole body to evaluate the interplay between exogenous dietary loads and endogenous demands of somatic tissue in each species. We hypothesized that early sexual maturation in reindeer and caribou is associated with more rapid growth in comparison with muskoxen and that somatic growth is related to an early maturation of nutritional organs for consumption of forage.

MATERIALS AND METHODS

Animals and feeding practices.—This study used only captive animals from the same location to minimize environmental differences between species and to remove any nutritional constraints on growth. All animals were from captive herds at the Robert G. White Large Animal Research Station and the Biological Reserve, Fairbanks, Alaska (65°N, 146°W), maintained by the Institute of Arctic Biology, University of Alaska Fairbanks for >15 years. Young animals remained with their mothers throughout the study and were able to consume milk naturally. All animals had access to fresh grass (*Bromus*) and browse (*Betula*, *Salix*) in their enclosures. Adult muskoxen were given grass hay (*Bromus*—Peltier et al. 2003) and a pelleted supplement of minerals (Muskox supplement—Rombach et al. 2002). Young muskoxen could access adult foods and a complete diet formulated from barley, corn, alfalfa, soy meal, and fish meal with minerals and vitamins (dry matter: lipid, 3.2%; neutral detergent fiber,

28%; lignin, 1%; carbon, 44.5%; nitrogen, 2.7%—Rombach et al. 2002). Reindeer and caribou were provided with a complete pelleted ration similar to that of young muskoxen. These feeds provided nutrient compositions similar to sedges, grass, and browse consumed by animals in the wild and thus provided captive animals with stimuli similar to their wild counterparts for development and growth (Jorgenson et al. 2002; Ohlson and Staalnd 2001). Animals were weighed (± 0.1 kg) on electric scales at regular intervals to monitor health and growth.

Total body growth.—We used repeated measures of body mass from birth to maturity to assess overall growth in each species. Data on the body mass of caribou ($n = 3$) and reindeer ($n = 3$) were available at 90-day intervals from birth (caribou, total of 18 weigh dates, castrated <5 months; reindeer, total of 30 weigh dates, castrated at 1 year). Weights from muskoxen ($n = 5$) were collected weekly from birth (total of 1,464 weigh dates, castrated at 1 year). Body mass included the mass of antlers in reindeer and caribou and horns in muskoxen.

Growth of body mass was described by fitting mass to age with the Gompertz growth equation (Zullinger et al. 1984) through a 3-parameter, nonlinear model: $M(t) = A \times e^{-e^{-K(t-I)}}$, where t = age (days), $M(t)$ = mass (g), A = asymptotic mass, K = growth constant (day^{-1}), and I = inflection point. Age at inflection was the point at which mass gains begin to slow and, therefore, provided an index of the time for maximal postnatal growth. The Gompertz equation was chosen because it provided less-biased estimates of growth in mammals when compared with von Bertalanffy and logistic equations (Zullinger et al. 1984). Data were fit using the nonlinear model function in Systat 10.2 (SPSS Inc., Chicago, Illinois). Iteration starting points were set to 0 for estimation of parameters A , K , and I . Calculation of the growth equations were performed through least-squares estimation by the Gauss-Newton method.

Growth of body components.—Growth of body components and hormones in young muskoxen were compared with young reindeer only because both species were born during the same month and, therefore, experienced the same window of growth until the 1st winter. We also compared reindeer with caribou at the same age (30 days) to assess any differences between the subspecies. Animals were necropsied after birth to assess postnatal development during the neonatal period (day 1–30) when milk was the primary food and in the subsequent period of transition to forage (day 30–60). Males and females were included in each group of young animals. Because digestive morphology of adults could be altered by reproductive status in these species (Barboza and Bowyer 2000, 2001), castrated caribou and muskoxen, 7 ± 2.5 years (mean age \pm SD) were used to represent the intermediate, mature state between intact males and females. One-day-old muskoxen ($n = 7$) were from a cohort born April–June 1999 (Rombach et al. 2002), whereas other young muskoxen were born April 2001 (30 days, $n = 4$; 60 days, $n = 4$). Young reindeer (1 day, $n = 4$; 30 days, $n = 4$; 60 days, $n = 3$) were born April 2002, and caribou (30 days, $n = 4$) were born June 2002. Adult castrates were taken for necropsy at similar times to young animals to minimize effects of season (April 2002 for muskoxen, $n = 5$; June 2002 for caribou, $n = 3$).

All animals were immobilized with tiletamine hydrochloride and zolazepam (3 mg/kg; Telazol 100 mg/ml, Fort Dodge Animal Health, Fort Dodge, Iowa) for transport to the necropsy facility. Blood was collected from the jugular vein into sterile evacuated glass tubes (Vacutainer, Becton Dickinson, Rutherford, New Jersey). Plasma was separated by centrifugation at $1,000 \times g$ and stored at -20°C for subsequent hormone analyses. Thirty and 60 day-old animals were maintained under anesthesia with isoflurane in oxygen for 2 h before euthanasia. The anesthetic period was used to equilibrate a dose of labels for measures of cell division for another study. Animals were euthanized by an overdose of barbiturates (Euthasol, Delmarva

Laboratories, Midlothian, Virginia) at the jugular vein. All procedures were approved for humane treatment of animals by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and in accordance with American Society of Mammalogists guidelines (Animal Care and Use Committee 1998).

Dissection of tissues commenced immediately after cardiac arrest and the loss of the corneal reflex. Digestive tract, liver, kidneys, and thyroids were excised and depleted of connective and adipose tissues before being weighed (± 0.01 g) on an electronic balance. Mass of paired organs (e.g., kidneys) was recorded as the sum of the pair. The digestive tract was ligated and measured as segments of the fore-stomach, small intestine, and hindgut. The fore-stomach was further divided into the reticulo-rumen (rumen), omasum, and abomasum. Samples were taken from the ingesta of the rumen and abomasum to describe the transition in dietary material (milk, forage, or pelleted supplement). The proximal colon and cecum (cecum) was the region from the ileo-cecal junction to the spiral colon. Distal colon (colon) included the tissue from the spiral colon to the rectum. Segments of the digestive tract were weighed with and without digesta to estimate the mass of contents. Ingesta-free mass was determined by subtracting the sum of digesta content from body mass.

Lipid content was evaluated from liver and skeletal muscle to evaluate lipid storage during maturation of tissues. Liver samples were collected from the caudate lobe in each animal. Samples of skeletal muscle were taken from the superficial gluteus of all animals except 1-day muskoxen, which was collected from the latissimus dorsi. Samples from both latissimus dorsi and superficial gluteus were taken from adult muskoxen and were used to assess differences in lipid content between muscle groups. All samples were stored at -20°C before analysis. A portion of each tissue (1 g) was thawed, weighed, and dried to constant mass in a 55°C oven for estimation of dry matter. Remaining tissue (>20 g) was freeze-dried to constant mass and homogenized for analysis. Lipid content was determined by petroleum-ether extraction (Soxtec No. 1043 Extractor, Tecator, Hoganas, Sweden).

Plasma was measured for total and free thyroxine (T4) and total and free triiodothyronine (T3) by solid-phase radioimmunoassay. Hormones bound to proteins in circulation, therefore, were the difference between total and free concentrations for T3 and T4. Concentrations of hormone were detected with rabbit antisera (Coat-A-Count, Diagnostic Products Corporation, Los Angeles, California) with iodinated (^{125}I) tracers. Effects of immobilants on concentrations of thyroid hormones were likely negligible because plasma was sampled within 45 min of immobilization. Hormone assays were replicated to within a 10% coefficient of variation (CV) for each blood sample. Each assay was validated for the recovery of iodinated hormone with plasma from each species containing hormone concentrations at the top and bottom of the calibration range. Recoveries of spiked assays were high and similar between species for total T4 (99%), total T3 (96%), free T4 (95%), and free T3 (91%). Consequently, we report hormone concentrations without adjustment for recovery in the assay.

Statistics.—Statistical analyses were performed using Systat 10.2 (SPSS Inc., Chicago, Illinois) with $\alpha = 0.05$. Parameters of Gompertz growth curves were considered similar if 95% confidence intervals (CI) overlapped. Postnatal growth was linear ($R^2 > 0.92$, $P < 0.001$, $n = 26$) over the first 60 days; therefore, daily mass gain (g/day) of components was estimated from neonatal (1–30 days) and transitional (30–60 days) periods. Daily mass gains of each component were compared between species and periods using chi-square statistics with Yates correction for 1 degree of freedom (*d.f.*—Fowler et al. 2003). Maturation of the fore-stomach was determined through examination of the proportions of rumen, omasum, and abomasum within each age group. Proportions of fore-stomach segments were normalized with an

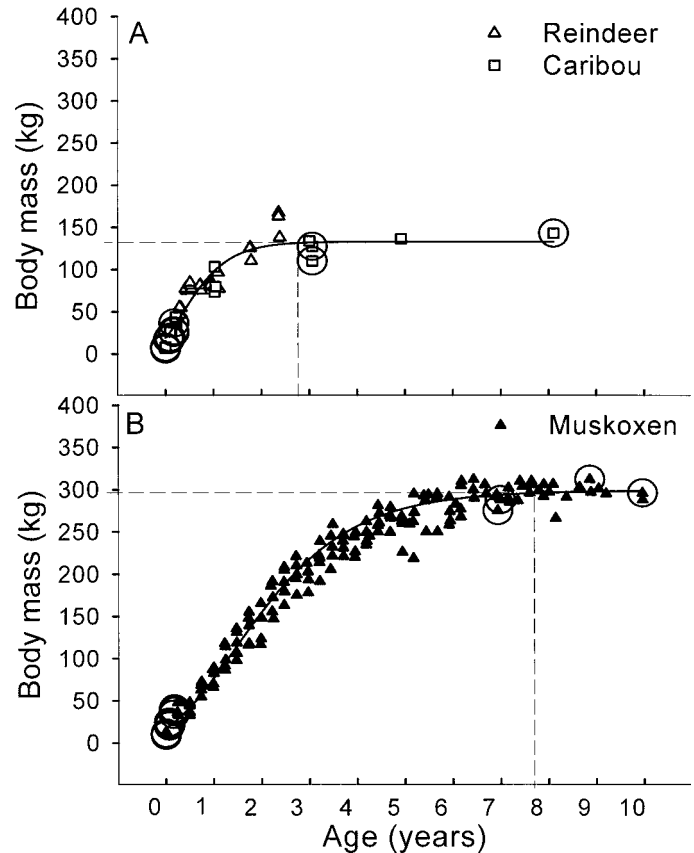


FIG. 1.—Growth of body mass (kg) of a) *Rangifer tarandus* (reindeer, caribou) and b) *Oribos moschatus* (muskoxen) fitted to the Gompertz equation for age (years), Fairbanks, Alaska, 1999–2002. Reindeer ($n = 3$) and caribou ($n = 3$); asymptotic mass (A) = 133 kg, growth constant (K) = 0.005 day^{-1} , inflection point (I) = 0.4 years, $R^2 = 0.958$; and Muskoxen ($n = 5$); A = 299 kg, K = 0.002 day^{-1} , I = 1.4 years, $R^2 = 0.970$. Body mass of muskoxen are shown at 90-day intervals. Dashed line indicates time to A. Circles in each graph indicate animals used for measures of body components (*Rangifer* $n = 14$ and muskoxen $n = 20$).

arcsine-square root transformation (Zar 1999). Only liver and kidney mass increased with body mass; therefore, we tested whether species and ages differed in the mass of liver and kidney while accounting for differences in body mass with analysis of covariance (ANCOVA; covariate is the ingesta-free mass minus the organ—Christians 1999). We used analysis of variance (ANOVA) to test effects of species and age on the mass of gastrointestinal segments, hormone concentrations, and lipids in tissues. Post hoc tests for species differences within an age group were performed using Bonferroni adjustments for multiple comparisons. Data are shown as mean \pm SD.

RESULTS

Both subspecies of *R. tarandus* grew at similar rates (reindeer: K = 0.004 day^{-1} , CI = $0.001\text{--}0.005 \text{ day}^{-1}$; caribou: K = 0.003 day^{-1} , CI = $0.003\text{--}0.005 \text{ day}^{-1}$) with inflection of growth occurring during the 1st winter (reindeer, I = 172 days, CI = 79–264 days; caribou, I = 165 days, CI = 111–219 days; Fig. 1A). Although mature reindeer were marginally larger than caribou this difference was not significant (reindeer, A = 165 kg, CI =

TABLE 1.—Mass of total body, ingesta-free mass, total digesta, and organs of young and adult *Rangifer tarandus* and *Ovibos moschatus*, Fairbanks, Alaska, 1999–2002. Different letters in each row indicate significant differences between species and age groups (ANOVA except liver and kidney, which was ANCOVA; Bonferroni adjusted $P < 0.05$).

	Age							
	1 day		30 days		60 days		Adult	
	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>
Body mass (kg)								
<i>R. tarandus</i>	6.86a	0.87	18.03a	1.16	29.70b	5.94	126.83c	16.60
<i>O. moschatus</i>	10.26a	0.84	22.63b	1.93	37.55b	2.78	291.80d	13.57
Ingesta-free mass (kg)								
<i>R. tarandus</i>	6.75a	0.86	17.02ab	1.31	27.63ab	5.71	115.52c	17.05
<i>O. moschatus</i>	10.13a	0.89	21.55ab	1.97	33.47b	2.22	253.47d	14.96
Digesta (kg)								
<i>R. tarandus</i>	0.01a	0.70	0.88a	0.24	2.07ab	0.24	11.31c	0.45
<i>O. moschatus</i>	0.13a	0.10	1.19a	0.14	4.08b	0.58	41.77d	2.77
Rumen (g)								
<i>R. tarandus</i>	32.45a	3.70	189.50a	66.00	668.00a	98.71	3285.50b	933.80
<i>O. moschatus</i>	59.07a	5.73	214.75a	12.12	652.25a	111.66	5640.00c	687.75
Omasum (g)								
<i>R. tarandus</i>	6.15a	1.43	17.15ab	2.68	37.77b	10.34	146.83c	53.09
<i>O. moschatus</i>	11.36a	2.87	31.00ab	1.63	56.33b	5.47	799.60d	56.09
Abomasum (g)								
<i>R. tarandus</i>	37.54a	1.35	86.01a	14.34	157.17b	33.33	353.50c	43.79
<i>O. moschatus</i>	46.43a	11.31	113.26a	12.95	157.25b	5.17	671.96d	103.96
Small intestine (g)								
<i>R. tarandus</i>	164.02ab	49.30	471.61bc	146.08	587.37c	112.34	728.06c	213.80
<i>O. moschatus</i>	206.41ab	58.41	616.20c	65.97	1317.57d	185.87	2056.45e	214.51
Cecum (g)								
<i>R. tarandus</i>	13.06a	2.33	62.00a	7.62	83.90ab	12.80	270.83b	36.29
<i>O. moschatus</i>	30.93a	17.69	53.25a	7.81	105.13ab	19.02	584.50c	196.25
Colon (g)								
<i>R. tarandus</i>			136.62a	32.36	243.23ab	21.86	1420.73b	456.64
<i>O. moschatus</i>	46.35a	25.23	219.52a	82.67	468.97ab	83.16	2044.17c	830.59
Liver (g)								
<i>R. tarandus</i>	174.97a	34.06	416.25b	35.88	681.33c	146.08	1677.5abc	207.85
<i>O. moschatus</i>	192.86ab	14.38	483.48b	30.47	707.13c	49.62	2203.7abc	158.87
Kidney (kg)								
<i>R. tarandus</i>	41.32a	6.75	87.86a	8.44	118.57a	13.54	361.75a	93.50
<i>O. moschatus</i>	41.64a	3.85	116.31a	13.36	143.73a	9.23	410.28b	19.81
Thyroid (kg)								
<i>R. tarandus</i>	2.94a	0.46	2.82a	0.29	3.48a	0.55	12.69b	3.53
<i>O. moschatus</i>	1.93a	0.35	2.52a	0.30	2.82a	0.27	17.76c	1.42

125–205 kg; caribou, $A = 132$ kg, $CI = 120$ – 144 kg). Similarities between reindeer and caribou in body growth and development of organs at 30 days of age (all organs, $P > 0.05$) indicate that the subspecies grow consistently even though birth dates may differ. Growth rate in muskoxen was also within the 95% confidence interval of reindeer and caribou during postnatal growth ($K = 0.002$ day⁻¹, $CI = 0.002$ – 0.003 day⁻¹). Growth inflection, however, was later ($I = 520$ days, $CI = 511$ – 528 days) and asymptotic mass was greater ($A = 299.3$ kg, $CI = 297$ – 301 kg) for muskoxen than that for reindeer and caribou (Fig. 1b).

Total body and ingesta-free mass of young and adult animals showed that muskoxen were larger than reindeer and caribou

overall ($F = 228.04$, $df. = 3, 30$, $P < 0.001$; Table 1). However, young muskoxen and reindeer were similar in size (Bonferroni-adjusted $P > 0.9$; Table 1). In proportion to maternal mass, reindeer also gave birth to larger young than did muskoxen ($6.9 \pm 1.0\%$ compared with $4.8 \pm 0.3\%$; $t = 61.8$, $df. = 19$, $P < 0.001$). Birth mass of reindeer were 5.4% and muskoxen were 3.5% of the mass of adult castrates. Reindeer continued to be proportionately larger than muskoxen (23% compared with 13% of adult mass) during the transitional period at 60 days of age (Table 1).

Young animals gained ingesta-free mass and increased digesta content during the neonatal period from 1 to 30 days,

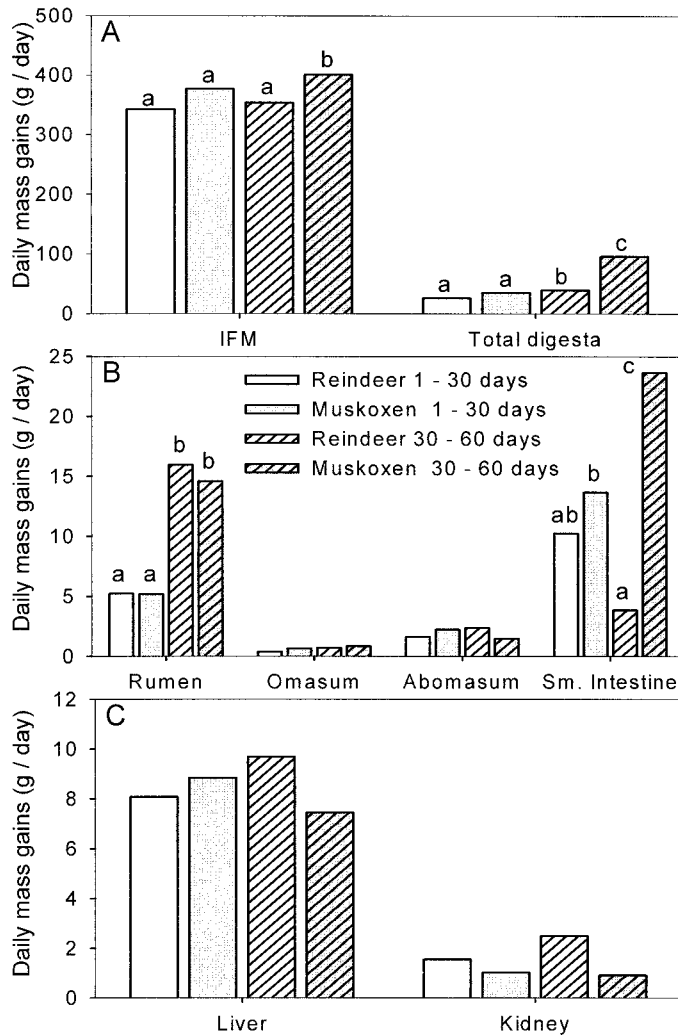


FIG. 2.—Daily mass gain (g/day) of body components of *Rangifer tarandus* (reindeer) and *Ovibos moschatus* (muskoxen) during milk consumption in the neonatal period (1–30 days) and while young transition to forage (30–60 days), Fairbanks, Alaska, 1999–2002. Different letters within each group indicate differences in mass gained ($\chi^2 > 3.8$; $d.f. = 1$; $P = 0.05$).

and in the transitional period from 30 to 60 days (Fig. 2A). Daily gains of ingesta-free mass were similar between species during the neonatal period ($\bar{X} = 348.1$ g/day; $\chi^2 = 3.2$, $d.f. = 1$, $P > 0.05$). Muskoxen increased gains of ingesta-free mass during the transitional period, whereas reindeer continued to grow at the same rate as in the neonatal period (reindeer = 353.8 g/day, muskoxen = 401.2 g/day; $\chi^2 = 6.2$, $d.f. = 1$, $P < 0.05$). Muskoxen also gained more mass than reindeer as digesta during the transitional period (reindeer = 35 g/day; muskoxen = 96 g/day; $\chi^2 = 6.2$, $d.f. = 1$, $P < 0.05$). Greater increases in digesta mass in muskoxen resulted in ingesta-free mass that was lower than total body mass by 17% for adult muskoxen and by 7% for adult caribou (Table 1).

Gains of ingesta-free mass in young reindeer and muskoxen were mainly associated with gains in lean rather than lipid mass. Newborn animals of both species had low concentrations of

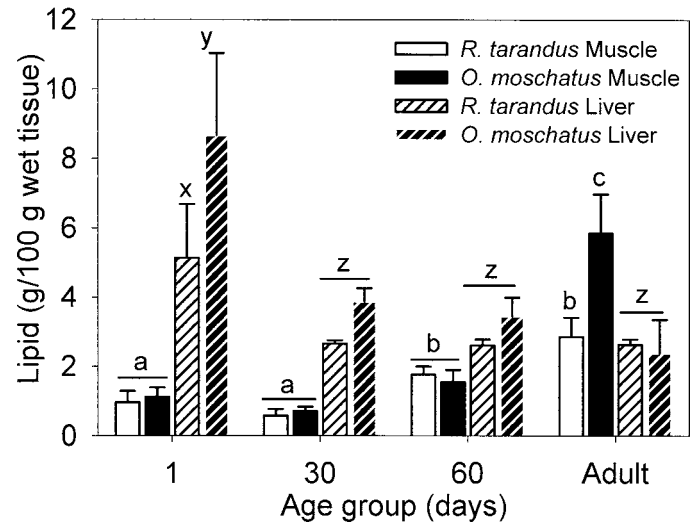


FIG. 3.—Lipid concentration (g lipid/100 g wet tissue, mean + SD) of liver and skeletal muscle from young and adult *Rangifer tarandus* and *Ovibos moschatus*, Fairbanks, Alaska, 1999–2002. Different letters indicate differences between species and age groups for muscle (a–c) or liver (x–z; Bonferroni-adjusted $P < 0.05$).

intramuscular lipid (1.0 g/100 g wet muscle) and continued to be lean to 30-days of age (0.7 g/100 g wet muscle; Fig. 3). Although superficial gluteus contained more lipid than the latissimus dorsi in adult muskoxen (5.8 compared with 3.5 g/100 g wet muscle; $F = 5.72$, $d.f. = 1, 8$, $P = 0.04$), lipid concentration of the gluteus in newborn muskoxen was likely similar to the low concentrations observed for the latissimus. Both species increased intramuscular lipid concentrations from 30 to 60 days during the transition to forage (1.7 g/100 g wet muscle; Bonferroni-adjusted $P < 0.006$; Fig. 3). Muscle lipid of 60-day-old reindeer and muskoxen were similar to adult caribou (Bonferroni-adjusted $P > 0.9$); however, adult muskoxen had a greater intramuscular lipid content than all young animals (Bonferroni adjusted $P < 0.001$).

Although intramuscular lipid was low and similar between species in newborn animals, lipid concentration of the liver in newborn animals was higher than muscle and greater in muskoxen than reindeer (8.7 compared with 5.1 g/100 g wet liver; Bonferroni-adjusted $P < 0.008$; Fig. 3). Lipid content of the liver declined by more than one-half in each species by 30 days (muskoxen = 3.9, reindeer = 2.6 g/100 g wet liver) and was similar to adult levels (Bonferroni-adjusted $P > 0.9$; Fig. 3). Absolute lipid content of the liver, however, increased with age and was greater in muskoxen than reindeer or caribou (1 to adult: 16.8–52.9 compared with 8.9–43.6 g/whole wet liver).

High lipid concentration of the liver in newborn animals corresponded to elevated levels of hormones in both species. Concentrations of T4 and free T3 were greater in newborn reindeer than in muskoxen ($P < 0.001$; Figs. 4A, 4B and 4D), even though thyroid mass did not differ between species in young animals (Bonferroni-adjusted $P > 0.9$; Table 1). Although thyroidal mass was greater in adult muskoxen than in adult caribou (Bonferroni-adjusted $P < 0.05$; Table 1), total concentrations of T4 were still higher in mature caribou than in

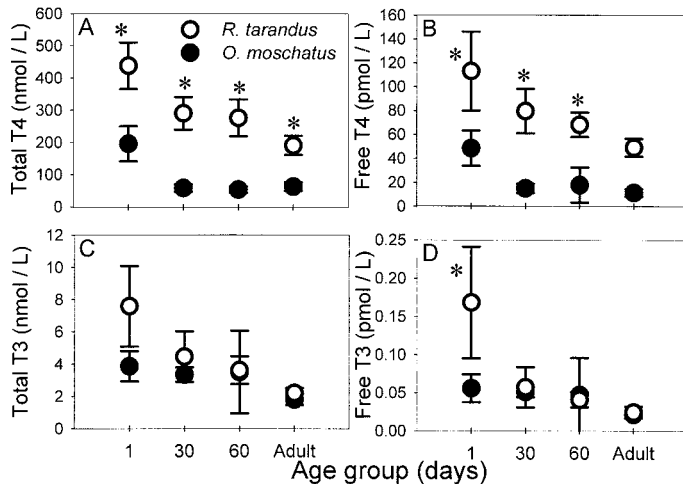


FIG. 4.—Thyroid hormone concentrations (mean \pm SD) in plasma from young and adult *Rangifer tarandus* and *Ovibos moschatus*, Fairbanks, Alaska, 1999–2002. Asterisks indicate significant differences between species (Bonferroni-adjusted $P < 0.05$) within age groups.

muskoxen ($P = 0.015$; Figs. 4A, 4B). Thus, plasma hormone levels were greater in reindeer and caribou than in muskoxen overall (species effect, $F > 6.2$, $d.f. = 1, 32$, $P < 0.02$) and declined with age in both species (age effect, $F > 9.9$, $d.f. = 3, 30$, $P < 0.001$; Fig. 4). Most circulating T4 and T3 were bound to carrier proteins (bound hormone = total – free) because only $<1\%$ were in the free form for both species at all ages. Concentrations of free T3, which would be most active at target tissues, were greater in newborn reindeer than muskoxen (1.7 ± 0.10 compared with 0.06 ± 0.02 nmol/liter; Bonferroni-adjusted $P < 0.05$), but declined to similar levels during the transitional period (0.06 nmol/liter) and into adulthood (0.02 nmol/liter; $P < 0.001$; Fig. 4D).

Young reindeer and muskoxen consumed similar diets at each postnatal age group. One-day-old animals had empty rumens, and abomasas that were filled with milk curds. Ruminal ingesta at 30 days consisted of soil and hair with remnants of milk, whereas the ingesta from the abomasum continued to contain milk curds. Ingesta of the rumen and abomasum at 60 days appeared similar to adult ingesta, which contained pelleted rations and pasture plants. The appearance of adult food items at 60 days coincided with gains of digesta mass during this transitional period (Fig. 2A).

The transition in diet also was reflected in the mass gains of the fore-stomach, which was similar between species. The rumen and abomasum in 1-day-old animals were similar in mass (Table 1) and contributed equal proportions to the fore-stomach (Fig. 5). Mass of the omasum was absolutely and proportionately larger in muskoxen than in reindeer at birth and all subsequent ages (species effect, $F = 335.2$, $d.f. = 1, 32$, $P < 0.001$; Table 1; Fig. 5). Mass gains were similar between neonatal and transitional periods for both omasum (<0.9 g/day) and abomasum (<2.4 g/day; $\chi^2 < 0.2$, $d.f. = 1$, $P > 0.05$; Fig. 2B). Gains of ruminal mass (5 g/day) exceeded rates of



FIG. 5.—Proportional mass of the abomasum, rumen, and omasum (percentage of total fore-stomach mass) for young and adult *Rangifer tarandus* (solid bars) and *Ovibos moschatus* (hatched bars), Fairbanks, Alaska, 1999–2002.

omasal and abomasal growth during the neonatal period. Ruminal growth was further enhanced as digesta mass increased during the transitional period (>15 g/day; $\chi^2 > 15$, $d.f. = 1$, $P < 0.01$; Fig. 2B). Thus, the abomasal proportion of the fore-stomach declined from 1 day to 60 days (50% to 10%; $F = 233.7$, $d.f. = 3, 30$, $P < 0.001$) whereas the ruminal proportion increased through the transitional period (50% to 70%; $F = 228.2$, $d.f. = 3, 30$, $P < 0.001$; Fig. 5).

Growth of intestinal mass also was high and associated with the transition to forage in both species. Although muskoxen had greater small-intestinal mass than reindeer (species effect, $F = 128.1$, $d.f. = 1, 32$, $P < 0.001$; Table 1), daily gains of the small intestine were similar between species during the neonatal period (12 g/day; $\chi^2 = 0.8$, $d.f. = 1$, $P > 0.05$; Fig. 2B). Muskoxen increased mass of the small intestine during the transitional period (23.4 g/day; $\chi^2 = 6.2$, $d.f. = 1$, $P < 0.05$) as digesta mass increased, whereas reindeer intestine continued to grow at a rate similar to the neonatal period (3.9 g/day; $\chi^2 = 3.4$, $d.f. = 1$, $P > 0.05$; Fig. 2b). Cecal and colonic mass also were greater in muskoxen than reindeer during neonatal and transitional periods (Bonferroni-adjusted $P < 0.001$; Table 1). Daily mass gains of the cecum did not differ between periods or species (<2 g/day; $\chi^2 < 0.4$, $d.f. = 1$, $P > 0.05$). Colon mass gain of muskoxen doubled during the transitional period (8.3 g/day) and was greater than colonic gains in reindeer (4 g/day; $\chi^2 = 5.2$, $d.f. = 1$, $P < 0.05$), whereas reindeer had similar mass gains of the colon between periods (<4 g/day; $\chi^2 < 0.1$, $d.f. = 1$, $P > 0.05$).

Growth rate of liver and kidneys did not differ between species or between neonatal and transitional periods (Fig. 2C). Rather, mass of the liver and kidneys followed increases in body mass (net ingesta-free mass as covariate, $F > 14.0$, $d.f. = 1, 32$, $P < 0.001$), and also increased with age independently of body mass ($F > 8.9$, $d.f. = 3, 30$, $P < 0.001$; Table 1). Young reindeer and adult caribou had larger kidneys for their body mass than muskoxen overall ($F = 8.0$, $d.f. = 1, 32$, $P < 0.009$),

but liver mass was similar between species at all ages ($F = 2.4$, $d.f. = 1, 32$, $P = 0.131$; Table 1).

DISCUSSION

Our hypothesis of more rapid somatic development in reindeer than muskoxen was supported by the proportionately greater birth mass of reindeer (6.9% compared with 4.8% maternal mass). This larger birth mass indicates that reindeer invest more energy and nutrients in the fetus during gestation. Size of reindeer and caribou neonates may ultimately reflect the minimal body size for mobility and thermoregulation in an ungulate that is highly active after birth (Klein 1991). High maternal investment of reindeer and caribou also is consistent with the close relationship between maternal body mass and the likelihood of parturition, as well as perinatal survival of offspring (Cameron et al. 1993; Whitten et al. 1992). Lower maternal investment in muskoxen could be related to the low-quality diet of sedges consumed by female muskoxen during early gestation, especially during winter when maternal demands for energy and nutrients greatly exceed food intake (White et al. 1989). Because gestational costs and gains of fetal mass in muskoxen are greatest in late winter (Rombach et al. 2003), low plant availability could be detrimental to fetal growth and survival of offspring. The combined effects of austere winters and short summers likely constrain maternal investment in arctic species because ruminants from more temperate regions give birth to proportionately larger offspring (white-tailed deer, *Odocoileus virginianus*, 11%; red deer, *Cervus elaphus*, 7.5%; African buffalo, *Syncerus caffer*, 7.5%—Robbins and Robbins 1979). Thus, selection for survival and future reproductive output by females may be more favorable than immediate investment in the fetus among arctic ruminants.

Low birth mass of arctic ungulates, therefore, may require greater thermogenic output in species that are born into low ambient temperatures. High levels of thyroid hormones in reindeer and muskoxen at birth are consistent with elevated rates of energy metabolism. Small absolute birth mass, however, may increase demands for thermogenesis in reindeer and caribou above those for muskoxen. Elevated thyroid hormones of neonates are consistent with development and maintenance of endothermy in several vertebrates (Laburn et al. 2000; McNabb et al. 1998) and are likely associated with a wide distribution of brown adipose tissue in young arctic ungulates (Blix et al. 1984; Soppela et al. 1992). High proportions of protein-bound hormone in both reindeer and muskoxen provide a large reservoir in circulation for release of free thyroidal hormones that could continue to integrate metabolic responses to exogenous demands through summer to increase growth and food intake at all ages (Nilssen et al. 1994; Ryg and Jacobson 1982). Elevated levels of T4 in reindeer at 30 and 60 days indicate that metabolic rates may exceed those of muskoxen during growth. Those differences, however, may reflect the kinetics of interconversion and excretion of thyroidal hormones and await direct confirmation from studies of receptor kinetics and binding of labeled T3 and T4 in these ruminants.

The large decline in hepatic lipid was probably associated with a change in metabolic function within the first days after birth. In utero sequestration of nutrients such as copper (Rombach et al. 2003) are consistent with the role of the liver as a reservoir of nutrients for early growth when milk intakes are low. The greater concentration of lipid in liver of muskoxen compared with reindeer may indicate differences between the species in intermediary metabolism and in the mobilization of lipids (Soppela and Nieminen 1998). Growth of liver, as well as kidneys, would also reflect changes in metabolic demands to support greater body mass (Adamczewski et al. 1987; Gerhart et al. 1996), in addition to the genetically determined size of the organ.

Our hypothesis of more rapid growth in reindeer and caribou than muskoxen was not supported by patterns of whole-body growth or ingesta-free mass because species grew at similar rates. Similarities in growth rate to 30 days of age probably reflect consumption of similar amounts of energy and protein in milk (Parker et al. 1990). High mass-specific milk intakes by reindeer in the first week of life (Parker et al. 1990) may reflect high metabolic rates associated with elevated thyroid hormones. Therefore, early growth of arctic ungulates can be limited by the lactational output of their mothers, even though milk is concentrated and high in energy content (Oftedal 1984; White and Luick 1984). These similarities are also probably associated with the consistent size of the abomasum at birth because that segment is a prerequisite for processing the first load of dietary protein and lipid (Thivend et al. 1984).

Growth of the reticulo-rumen and the intestines may be influenced most by the fill and composition of ingesta that change dramatically in the transition from milk to a diet high in vegetation. Ingestion of hair and soil by young arctic ungulates at 30 days of age could be an inadvertent consequence of suckling behavior but also may be part of the mechanism to stimulate the differentiation of mucosa before ingestion of plant fiber. Gains in ruminal mass of both species coincide with the presence of forages in ruminal ingesta and an apparently active fermentation system. Physical stimulus of ingesta combined with the chemical stimuli of fermentation products would promote further rumen expansion as young animals consume greater amounts of forage (Faurie and Perrin 1995; Lentle et al. 1996; Soveri and Nieminen 1995; White et al. 1984). Therefore, rapid growth rates of young arctic ungulates after the transition to forage could be limited by the quality and abundance of forage plants (Lindsay et al. 1993; McEwan 1968; Olesen et al. 1991; Reimers et al. 1983).

Maximal size and structure of the fore-stomach is a species-specific attribute (Langer 1988), which ultimately determines the capacity of the ruminal fermentation as the animal grows (Clauss et al. 2003). The relative functions of the rumen, omasum, and abomasum are well established by 60-days old in both reindeer and muskoxen because segmental proportions were similar to adults. The early establishment of foregut may be a common feature among ruminants because fore-stomach proportions of domestic ruminants are similarly advanced at this same age (Church et al. 1961; Lyford 1988). However, the absolute capacity of the rumen in relation to body size is small

(Barboza and Bowyer 2000, 2001). Body size and ruminal mass of reindeer and muskoxen at 60 days-old indicate that these species may have similar abilities to use fiber at the end of the 1st summer. The greater selection of forbs by young muskoxen compared with adults reflects the use of more digestible species among the available plants (Cote et al. 1997; Oakes et al. 1991). Greater consumption of sedges and grass in adult muskoxen may only occur as muskoxen continue to gain size and can increase fermentation of more fibrous forages. Large omasal mass in muskoxen at all ages, however, indicates a genetic attribute of the species (Langer 1988) that may, in part, determine the grazing feeding strategy of adults.

Young arctic ungulates, therefore, must transition to similar diets of growing plants well before those forages senesce, which would contribute to lean mass gains during summer. Small increments in muscle lipid during the first 60 days of life were probably associated with maturation of connective tissues and intracellular membranes (Dickerson and Widdowson 1960). Young arctic ungulates continue to remain lean throughout their first summer (Adamczewski et al. 1987, 1995; Peltier and Barboza 2003). Additions of muscle mass during the first summer, therefore, must provide enough energy to survive winter when food supply is limited. A rapid transition from milk to forage consumption by 60 days of age would allow young arctic ungulates to consume plants at early, phenological stages that contain the highest nitrogen content (Johnstone et al. 2002; Rachlow and Bowyer 1994) that could support these gains in lean mass. Early transition to forage would also enable young ungulates to consume forages during the entire growing season.

Delays in parturition may shorten the window for the transition to forage and force young animals to switch from milk to senescing plants that are high in fiber and most difficult to digest (Bowyer 1991). Later births in caribou as compared with reindeer could suggest differences between the subspecies in maternal investment and the importance of calving grounds or delays in plant emergence at high latitudes (Griffith et al. 2002; Loudon et al. 1989). Milk may also be a crucial supplement of energy during the transition to forage and in the first winter as young arctic ungulates may not digest winter forages as effectively as adults (Munn and Dawson 2003). The disparity between young and adult animals may, however, be smaller for more digestible foods such as lichens or browse that are favored by reindeer and caribou. Longer lactation periods in muskoxen, therefore, may provide additional nutrition in a species that has a greater growth period and takes longer to reach the ruminal capacity for consumption of adult forages.

Growth rates of ruminants in the Arctic are rapid but similar to those of African species (e.g., wildebeest, *Connochaetes taurinus*, $A = 220$ kg, $K = 0.002 \text{ day}^{-1}$; nyala, *Tragelaphus angasii*, $A = 105$ kg, $K = 0.005 \text{ day}^{-1}$ —Attwell 1982; Georgiadis 1985; Robbins and Robbins 1979). In fact, ruminant species are considered to have one of the most rapid growth rates among vertebrates (Case 1978). Differences between reindeer, caribou, and muskoxen in adult mass and sexual maturation, therefore, are a proximal outcome of the duration of growth and the number of growing seasons required to reach mature body mass (Adamczewski et al. 1997; Leader-Williams and Ricketts

1981). This hypothesis is supported by longer growth curves in males compared with females in Arctic ruminants and in other sexually dimorphic species (Georgiadis 1985; Peltier and Barboza 2003; Spaeth et al. 2001). Consequently, Zullinger et al. (1984) reported that female reindeer and muskoxen had a similar growth constant (K ; reindeer = 0.005 day^{-1} , muskoxen = 0.004 day^{-1}) but earlier inflection points (reindeer = 160 days, muskoxen = 360 days) than castrated males in this study. Therefore, endogenous rates of development may be more important than exogenous cues in determining maximal rates of growth in ruminants after nutrient demands are satisfied.

Similar rates of growth and organ maturation among young ruminants may ultimately reflect common endogenous cues and consumption of high-quality milk and forages. Rapid transition to forage would limit the requirement of maternal milk production and initiate an early dependence on forage for further growth. Transition to forage in species that consume more fibrous plants may require a longer time for expansion of specialized foreguts. Growth and organ maturation of ungulates, therefore, emphasizes maternal investment in utero and the duration of growth period with little variation in growth rate during both neonatal and transitional phases.

ACKNOWLEDGMENTS

Funding was provided by grants from the Alaska Science and Technology Foundation (Project #98-4-128) and the Institute of Arctic Biology to P. Barboza. Graduate fellowships for K. Knott were provided by the National Science Foundation (Alaska Experimental Program to Stimulate Competitive Research). We thank R. Kedrowski, K. Budsberg, and D. Johns for expert assistance in chemical analysis; J. Blake and C. Rosa for veterinary assistance; and all involved with animal care and handling at the Institute of Arctic Biology, including W. Hauer, C. Terzi, S. Pence, D. Hartbauer, R. Aikman, J. Jack, P. Reynoldson, and several volunteer assistants. We also thank 2 anonymous reviewers for their helpful comments on an earlier draft.

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Submitted 26 February 2004. Accepted 21 May 2004.

Associate Editor was Floyd W. Weckerly.