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The nitrogen window for arctic herbivores: plant phenology and protein gain of migratory caribou (*Rangifer tarandus*)

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Abstract. Terrestrial plants are often limited by nitrogen (N) in arctic systems, but constraints of N supply on herbivores are typically considered secondary to those of energy. We tested the hypothesis that forage N is more limiting than energy for arctic caribou by collecting key forages (three species of graminoids, three species of woody browse, and one genus of forb) over three summers in the migratory range of the Central Arctic Herd in Alaska from the Brooks Range to the Coastal Plain on the Arctic Ocean. We combined in vitro digestion and detergent extraction to measure fiber, digestible energy, and usable fractions of N in forages (n = 771). Digestible energy content fell below the minimum threshold value of 9 kJ/g for one single forage group: graminoids, and only beyond 64–75 d from parturition (6 June), whereas all forages fell below the minimum threshold value for digestible N (1% of dry matter) before female caribou would have weaned their calves at 100 d from parturition. The window for digestible N was shortest for browse, which fell below 1% at 30–41 d from parturition, whereas digestible N contents of graminoids were adequate until 46–57 d from parturition. The low quality of browse as a source of N was also apparent from concentrations of available N (i.e., the N not bound to fiber) that were <1% at 72–80 d from parturition. The Coastal Plain may be favored by female caribou because available and digestible concentrations of N are not only greater than those on the Brooks Range, the window of usable N on the Coastal Plain extends the period of protein gain for females and their calves by 17 d. Conversely, inland areas with greater biomass and densities of digestible N than the Coastal Plain may be more favorable for large male caribou that begin gaining protein from spring to breed in autumn. Our study provides evidence that phenological windows for protein gain in caribou are both spatially and temporally dynamic and likely to affect the distribution and growth of the population.

Key words: Arctic; browse; digestible energy; digestible protein; forage quality; graminoid; *Rangifer*.

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Introduction

Nutrients such as nitrogen (N) limit the growth of plants especially in arctic systems where the period of growth is confined to a short summer of <3 months (White and Luick 1984, Arndal et al. 2009, Fay et al. 2015). Winter precipitation and spring temperatures affect the onset and rate of plant growth in the Arctic, but the end of the season is ultimately limited by

light and photoperiod (Cooper 2014). The window for plant growth provides an annual pulse of food that drives herbivore populations (especially from the temperate zone to the Arctic), but that window starts later and ends earlier with increasing latitude to the high arctic (Huston and Wolverton 2009).

Air temperatures affect plant growth and thus the distribution of arctic herbivores. Gradual changes in average annual temperatures have advanced spring thaws and the duration of summer, which has increased plant biomass especially at high latitudes (van der Wal and Stien 2014). In Alaska, warming temperatures have been associated with the expansion of shrubs in the Arctic especially along riparian corridors (Sturm et al. 2001) that has supported a northward expansion of a large browsing ungulate, moose (*Alces alces*; Tape et al. 2016). Although advances in spring thaw have been associated with early arrival of migratory birds for nesting (Ward et al. 2016), parturition by migratory caribou (*Rangifer tarandus*) in the same region has not advanced (Gustine et al. 2017*a*). Arctic ungulates such as caribou and reindeer may be less influenced by the onset of spring and more affected by the duration of the window of plant availability in summer and the duration and severity of the preceding winter (Tveraa et al. 2013, Albon et al. 2016, Bårdsen 2017) because the window of plant growth is used to establish body stores for subsequent survival and reproduction (Barboza and Parker 2008).

Large herbivores use a diversity of movement strategies to track changes in the abundance and quality of their foods (Monteith et al. 2014, Aikens et al. 2017) while balancing the relative benefits for survival and reproduction (Fryxell and Holt 2013, Winkler et al. 2014). In the Arctic, annual movements of ungulates range from >3000 km for barren ground caribou (*R.t. granti*) to <100 km for muskoxen (*Ovibos moschatus*) and Svalbard reindeer (*R.t. playtrhynchos*; Fancy et al. 1989, Couturier et al. 2010, Schmidt et al. 2016). Migrations of caribou are affected by differences in the reproductive demands of males and females: Male caribou migrate shorter distances than female caribou, which aggregate for parturition (Cameron and Whitten 1979, Russell et al. 1993). The extent and the location of the calving areas used by females vary (Taillon et al. 2012, Miller et al. 2013) in response to changes in population size, weather conditions, and plant biomass (Cameron et al. 2002, Griffith et al. 2002, Schaefer and Mahoney 2013, Le Corre et al. 2017).

Arctic ungulates use body stores of energy and N in fat and protein to start pregnancy in winter and to support lactation in spring but must recover sufficient body stores over the summer to survive the next winter and establish the reserves for another reproductive cycle. Winter supplies of energy and N in forages are very low because food availability is limited by snow cover and because the N content of winter lichens and senesced vascular plants is low. The relative costs of reproduction are greater for N than for energy in reindeer and caribou: The minimum intake of N increases by 120%, whereas that of energy only increases by 50% in lactation (Barboza and Parker 2008). Caribou are able to conserve N over winter to produce a calf with N that was stored in the previous summer (Barboza and Parker 2006, 2008). In wild female caribou, over 90% of the protein in newborn calves and over 87% of milk protein are derived from body protein stores such as muscle, which is consistent with smaller body mass of calves in a herd with lower allocations of maternal protein (Taillon et al. 2013). Positive relationships between body mass of a calf and the mass of its mother in the previous year (Albon et al. 2016, Veiberg et al. 2016) are consistent with a strong role of N stores for reproduction in caribou and reindeer. The role of forage N in establishing body protein is also consistent with declines in fecundity, calf mass, and body size of caribou when populations attain high densities that reduce forage quality on the summer range (Crete and Huot 1993, Manseau et al. 1996, Couturier et al. 2009, 2010, Schaefer et al. 2016).

Although caribou and reindeer consume a wide variety of vegetation including fungi, lichens, woody browse, graminoids, and forbs (Thompson et al. 2015, Schaefer et al. 2016, Denryter et al. 2017), only a few items comprise most of the mass of the diet, especially in arctic regions where plant diversity is low. Total N content of plant tissues increases with the development of photosynthetic cells in spring and decreases through senescence in summer. Forage maturation is associated with deposition of structural components of the fiber matrix (acid detergent fiber [ADF] and lignin) that are most resistant to chewing and digestion, which impairs the release of energy and nutrients

contained in the plant cell walls (neutral detergent fiber) as well as the contents of the plant cell. Caribou avidly select the N-rich flowers and emergent leaves of graminoids and forbs (Klein 1990, Jorgenson and Udevitz 1992), but only a fraction of N in plant tissues is available to the herbivore because N is bound in the structure of the fiber matrix and because plant secondary metabolites can directly bind protein or impair enzymes that digest proteins (Wallis et al. 2012). Selection of leaves may attenuate some of the phenological changes in fiber of graminoids and woody browse, but caribou may not be able to avoid phenolic plant secondary metabolites in browse (Thompson and Barboza 2014). Although caribou are able to tolerate fiber and plant secondary metabolites (Sundset et al. 2010, Thompson and Barboza 2014), phenolic anti-nutrients such as lignin and tannins ultimately reduce the energy and N in the forage that can be retained and used by the herbivore (Mithofer and Boland 2012, Stolter et al. 2013). Forages that provide <9 kJ/g or <1 gN/100 g after digestion are likely to impair lactating caribou and their calves (Barboza and Parker 2006, 2008, Hewitt 2011) because the ability to compensate for the low quality of these foods by increasing food intake is limited below these thresholds (Barboza et al. 2009).

We tested the hypothesis than forage N is more limiting than energy for arctic caribou. We studied three species of graminoids, three species of woody browse, and one genus of forb that are used by caribou to test the hypothesis that N and energy supplies differ among plant functional groups. We collected forages over three summers in the migratory range of the Central Arctic Herd in Alaska over three ecoregions from the Brooks Range mountains to the coast of the Arctic Ocean to test the hypothesis that N supply and energy supply vary with ecoregion and with time (i.e., year and day within year). We used an in vitro method to estimate digestion of dry matter, which was validated for caribou (Van Someren et al. 2015). The method does not use microbial extracts that colonize the surface of the sample or reagents that contaminate the residues with N (Gustine et al. 2014). We were, therefore, able to measure N in the residue to estimate the fraction of N that is resistant to digestion. We used extraction with acid detergent to estimate the structural proportion of the forage that is most resistant to digestion and to measure the N that is available outside the core of the fiber matrix. Here, we examine the phenology of N that is available to caribou from the cells and digestible structural tissues of the forage (available N) and the forage N that can be digested by acid and enzymes (digestible N). We use these two estimates of usable N to define an upper bound of available N that could be extracted from the forage and a lower bound of digestible N that is likely extracted by the secretions of the animal. We also describe the phenology of anti-nutrients (fiber and phenols) to index the chemical progression of the forage to senescence and the relationship between anti-nutrients and digestible N for caribou. Here, we provide evidence that digestible N is more limiting than digestible energy for caribou and that the window for building protein stores in caribou varies with ecoregion and year, which could affect the distribution and growth of the population.

Methods

This study was conducted from 2011 to 2013 in the summer range of the Central Arctic Herd of caribou on the North Slope of Alaska (Fig. 1; Whitten and Cameron 1980, Arthur and Del Vecchio 2009). We sampled nine sites spread evenly over a 200-km transect along the Dalton Highway from the Kuparuk River to Prudhoe Bay (Fig. 1) where caribou can be observed from spring to fall. Study sites were at least 1 km away from the road to avoid effects of dust and water runoff (Walker and Everett 1987). Sites were classified into three ecoregions: Brooks Range, Arctic Foothills, and Coastal Plain (Gallant et al. 1995, Gustine et al. 2017*a*). Caribou in this herd typically winter within or south of the Brooks Range before migrating northwards through the Brooks Range and Arctic Foothills to reach the calving grounds in the Coastal Plain ecoregion around 24 May (ordinal date 144; Arthur and Del Vecchio 2009, Nicholson et al. 2016). After giving birth, females typically spend the rest of the summer in the Coastal Plain ecoregion before slowly migrating southwards again (starting from 26 September, ordinal date 269) through the Arctic Foothills and Brooks Range during the fall breeding season (Cameron and Whitten 1979, Jakimchuk et al. 1987, Nicholson et al. 2016). Although males also use the Coastal Plain ecoregion, they generally

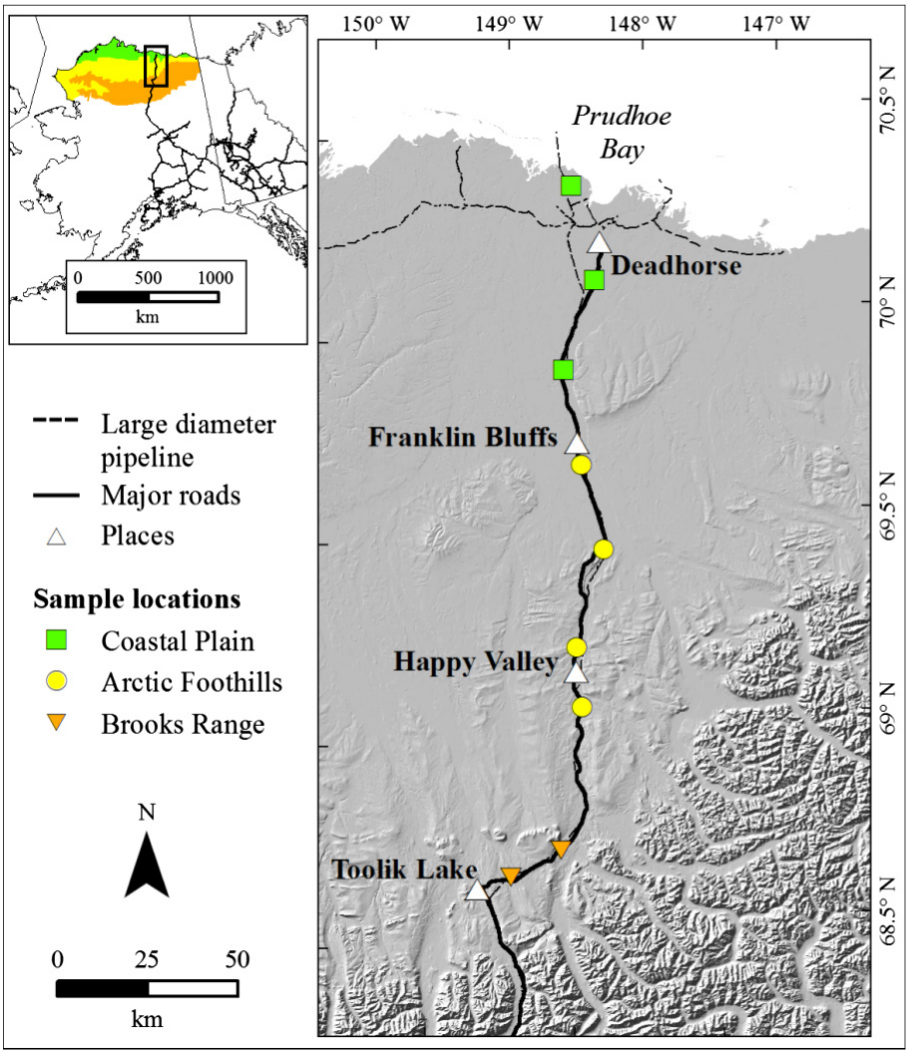

Fig. 1. Location of study sites within the range of the Central Arctic caribou Herd. Sites were located in three ecoregions (Coastal Plain, Arctic Foothills, and Brooks Range) along the Dalton Highway. The distribution of the Arctic ecoregions in Alaska is noted in the inset.

have a more southerly distribution than females during the growing season (Cameron and Whitten 1979, Jakimchuk et al. 1987). The Central Arctic Herd of caribou has been counted in summer from 1978. The maximum estimate of 68,442 animals was attained in 2010 before the start of this study with subsequent estimates at 50,753 animals in 2013 at the end of this study and 22,630 in 2016 after the study (Lenart 2015, Alaska Department of Fish and Game 2016).

Samples of six preferred forage species (*Carex aquatilis*, *Carex bigelowii*, *Eriophorum vaginatum*, *Pedicularis* spp., *Salix pulchra*, and *Salix richardsonii*; Thompson and McCourt 1981) were collected, when present, every two weeks from late May to late September. In addition, we collected samples of *Betula nana* in 2012 and 2013. Although this species of birch does not make up a large part of North Slope caribou diets at present, it may be eaten by caribou more frequently in the future because it is increasing in abundance throughout the Arctic (Sturm et al. 2001, Myers-Smith et al. 2011, Kaarlejarvi et al. 2012). Indeed, another birch, *B. glandulosa*, makes up a

significant part of caribou diets in Quebec (Crete et al. 1990, Zamin et al. 2017).

Forage plants were sampled for biomass and quality by mimicking caribou browsing and grazing, that is, for deciduous shrubs, easily accessible leaves and twigs were stripped off, while forbs and graminoids were clipped at ground level. Biomass was measured in 0.5 × 0.5 m quadrats at up to five locations within each site of 5 ha (Gustine et al. 2017*a*). Forage quality samples (20–100 g) were collected directly adjacent to biomass sites to preclude any effects of forage removal. Forage samples were transferred to pre-weighed paper bags and air-dried at ambient temperature (0–22°C) in the field and then air-dried to constant mass in a forced-air oven at 50–55°C when samples were returned to the laboratory, within 2–6 d of collection. Dried samples were ground through a #20 mesh (1.27 mm) in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA) or a centrifugal mill (Retsch ZM 200, Haan, Germany).

Laboratory Analyses

We measured the total N content in 771 forage samples with an elemental analyzer (CNS2000; LECO, St. Joseph, Michigan, USA). Phenology curves of total N vs. ordinal day (OD) were established for each species × site × year combination, and we used these curves to select representative samples for further analysis from three key time periods: early season (peak N content), mid-season (peak biomass), and late season (last sampling date; Gustine et al. 2017*a*). These samples were analyzed for dry matter content (DM) and neutral detergent fiber (total plant cell walls), ADF, and acid lignin (Van Soest et al. 1991; Barboza and Parker 2006). We measured digestibility (g digested/g whole) of dry matter by using an in vitro digestibility method with purified enzymes (DeGabriel et al. 2008), which has been validated for caribou (Van Someren et al. 2015). Digestible N (g/100 g DM) was estimated as the difference between total N and the N retained in the residue from in vitro digestion. Similarly, available N was calculated as the difference between total N and the N retained in the ADF residue. Gross energy content was determined using an adiabatic bomb calorimeter (Parr Instruments, Moline, Illinois, USA). Digestible energy content was calculated as the product of gross energy content and digestibility of DM. We measured total phenolic compounds by reaction of extracted phenolics with Folin–Ciocalteu reagent, which was expressed in gallic acid equivalents as a standard phenol (mg gallic acid/g DM; Singleton et al. 1999).

Statistical analyses

All analyses were conducted in Stata 15.0 (StataCorp, College Station, Texas, USA).

We used ordinary least-squares regression to compare fiber fractions (plant cell walls or lignin vs. ADF) and N fractions (available or digestible N vs. total N). The 95% confidence intervals for the estimates of the slope and the intercept of each regression were used to compare relationships among forages and to compare the relationships with unity (slope = 1, intercept = 0; Acock 2016). Estimates from regression models are presented as means with standard errors (SEs; $\bar{X} \pm$ SE).

We analyzed spatial and temporal variation among forages at two levels: species (n = 7) and functional group (n = 3). Plant functional groups consisted of graminoids (*C. aquatilis*, *C. bigelowii*, and *E. vaginatum*), browse (*B. nana*, *S. pulchra*, and *S. richardsonii*), and one genus of forb (*Pedicularis* spp.). Spatial variation was considered at two levels: ecoregion (Brooks Range, Arctic Foothills, and Coastal Plain) and sample site (n = 9). Temporal variation was included at two levels: year (2011, 2012, 2013) and OD within each year (days 148–269 or 28 May–26 September). We used mixed-effects regression to analyze spatial and temporal variation in plant components (i.e., Y = biomass, N fractions, fiber fractions, phenols, or digestible energy). Each model included sample site as a random effect to account for repeated sampling through the study. Fixed effects in the full model were as follows: year, ecoregion, OD, OD^2, plant, plant × OD, plant × OD^2. We used quadratic terms for ordinal date in the models because plant phenologies are often quadratic functions of ordinal date (Gustine et al. 2017*a*). Biomass was transformed to the square root for analysis (van der Wal and Stien 2014), but all other variables were analyzed without transformation. We used the robust "sandwich estimator" for SEs to relax assumptions of normal distribution and homogeneity of variances for mixed-model regressions (Rabe-Hesketh and Skrondal 2010). Model coefficients were compared with zero using a z test at $P < 0.05$. Linear fixed effects were examined with post hoc Wald tests on the chi-squared

statistic at $P < 0.05$. We removed fixed effects from the model when coefficients and post hoc linear tests were not significantly different from zero. Plants were modeled at the species level and the functional group level. Species-level models were used to plot phenological changes in plant components by estimating margins (mean ± SE) at ODs (Mitchell 2012). Similarly, functional group models were used to estimate margins for fixed effects, which were corrected by the Bonferroni method for multiple pairwise comparisons (Mitchell 2012). The effects of anti-nutrients on digestible N and digestible energy were analyzed at the species level with a mixed model that included the following fixed effects: year, plant, ADF, phenol, plant × ADF, plant × phenol.

We used dietary concentrations of 9 kJ/g (digestible energy) and 1 gN/100 g (available N and digestible N) as thresholds at which performance of lactating cervids and their calves is likely to be impaired (Barboza and Parker 2006, 2008, Hewitt 2011). Plant phenologies were compared with the reproductive phenology of the Central Arctic Herd based on an average date of parturition at 6 June (OD 157; Lenart 2015, Nicholson et al. 2016). Milk production of caribou cows is highest during early lactation (0–28 d from parturition) and declines through late lactation (White and Luick 1984, Parker et al. 1990, Gjostein et al. 2004) until calves are weaned after 100 d from parturition (Lavigueur and Barrette 1992, Parker and Barboza 2013). The range of days on which predicted concentration of a plant group fell below a threshold value was calculated from the 95% confidence intervals for daily estimates of digestible N or digestible energy as the days on which the lower and upper limits crossed the threshold.

Data disposition

Data are available from the U.S. Geological Survey: https://doi.org/10.5066/f7jq106w (Gustine et al. 2017*b*).

Results

Forage densities on the Brooks Range were three times greater than those on the Coastal Plain (Table 1). Graminoids provided the greatest biomass in each ecoregion (Table 1) at densities that were 1.7–2.5 times greater than those of the browse species and 10–1000 times greater than those of the forb (*Pedicularis* spp*)*. The highest biomass densities were associated with the graminoids *E. vaginatum* (7.9 ± 0.4 g/m^2) and *C. aquatilis* (5.82 ± 0.49 g/m^2), whereas the most abundant browse species were *B. nana* (3.94 ± 0.18 g/m^2) and *S. richardsonii* (3.13 ± 0.18 g/m^2). Densities of *Pedicularis* spp. (0.31 ± 0.09 g/m^2) were much lower than the least abundant graminoid (*C. bigelowii* at 2.73 ± 0.16 g/m^2) and the least abundant browse (*S. pulchra* at 1.21 ± 0.09 g/m^2). Biomass densities varied within each season (Fig. 2) and among years ($\chi^2 = 20.43$; 2 df; $P < 0.0001$) from an average of 2.99 g/m^2 (±0.03) in 2011 to 4.18 g/m^2 (±0.05) in 2012 to 2.21 g/m^2 (±0.03) in 2013. Average biomass density rose through the period of parturition and early lactation for caribou to reach maxima at OD 207, which was followed by rapid senescence in some species such as *B. nana* and *Pedicularis* spp. after OD 240 (Fig. 2).

Predicted concentrations of total N in forages declined from emergence of new growth (2.88 ± 0.04 gN/100 g at OD 157) through early summer (2.34 ± 0.05 gN/100 g at OD 175) to senescence in late summer (1.11 ± 0.05 gN/100 g at OD 257). Decreases in available N were directly related to those of total N in both graminoids ($Y = -0.20$ (±0.02) + $X \cdot 1.02$ (±0.01; 95% confidence intereval [CI]: 1.00–1.03); $R^2 = 0.99$) and browse species ($Y = -0.55$ (±0.06) + $X \cdot 0.98$ (±0.03; 95% CI: 0.93–1.04); $R^2 = 0.93$; Appendix S1: Fig. S1), that is slopes for both relationships overlapped 1.0. The digestible fraction of N was much smaller than the available fraction and declined more slowly with total N for both graminoids ($Y = -0.34$ (±0.04) + $X \cdot 0.72$ (±0.02; 95% CI: 0.68–0.76); $R^2 = 0.90$) and browse ($Y = -0.54$ (±0.10) + $X \cdot 0.62$ (±0.04; 95% CI: 0.54–0.70); $R^2 = 0.99$; Fig. 3). In the forb, relationships with total N were similar for available N ($Y = -0.34$ (±0.08) + $X \cdot 0.86$ (±0.04; 95% CI: 0.79–0.93); $R^2 = 0.93$) and for digestible N ($Y = -0.34$ (±0.08) + $X \cdot 0.90$ (±0.04; 95% CI: 0.83–0.98); $R^2 = 0.99$; Appendix S1: Fig. S1).

Although browse contained more total N than graminoids, available N was similar between browse and graminoids (Table 1) whereas digestible N was lower in browse than graminoids and greatest in the forb (Table 1). Predicted concentrations of digestible N fell below the

Table 1. Predicted ($\bar{X} \pm$ SE) biomass densities (g/m^2) and the concentrations of N (g/100g) and digestible energy (kJ/g) in the dry mass (DM) of three species of graminoids (*Eriophorum vaginatum*, *Carex aquatilis*, *Carex bigelowii*), three species of browse (*Betula nana*, *Salix pulchra*, *Salix richardsonii*), and one genus of forb (*Pedicularis* spp.) available to caribou in the summer range of the Central Arctic Herd (2011–2013).

Variable and ecoregion	Graminoids	Browse	Forb	Ecoregion means
Biomass (g DM/m^2) (n = 728)				
Brooks Range	7.91 ± 0.32 d	4.47 ± 0.13 bc	0.82 ± 0.09 a	5.05 ± 0.05 A
Arctic Foothills	5.07 ± 0.39 d	2.43 ± 0.15 b	0.11 ± 0.08 a	2.81 ± 0.08 AB
Coastal Plain	3.49 ± 0.35 cd	1.39 ± 0.16 b	0.00 ± 0.06 a	1.63 ± 0.10 B
Forage means	5.14 ± 0.35 A	2.31 ± 0.11 B	0.15 ± 0.03 C	
Total N (g/100 g DM) (n = 771)				
Brooks Range	1.82 ± 0.03 ab	2.14 ± 0.03 cd	1.74 ± 0.08 a	1.91 ± 0.02 A
Arctic Foothills	1.83 ± 0.03 ab	2.15 ± 0.04 cd	1.75 ± 0.08 a	1.91 ± 0.03 A
Coastal Plain	2.18 ± 0.14 bcd	2.50 ± 0.14 d	2.10 ± 0.21 abc	2.27 ± 0.15 A
Forage means	1.91 ± 0.04 A	2.23 ± 0.03 B	1.83 ± 0.11 A	
Available N (g/100 g DM) (n = 316)				
Brooks Range	1.68 ± 0.03 bc	1.62 ± 0.03 bc	1.19 ± 0.05 a	1.57 ± 0.02 A
Arctic Foothills	1.67 ± 0.03 bc	1.61 ± 0.03 bc	1.18 ± 0.05 a	1.55 ± 0.02 A
Coastal Plain	2.01 ± 0.13 c	1.94 ± 0.12 c	1.51 ± 0.17 ab	1.89 ± 0.13 B
Forage means	1.77 ± 0.04 A	1.71 ± 0.04 A	1.27 ± 0.08 B	
Digestible N (g/100 g DM) (n = 333)				
Brooks Range	0.98 ± 0.03 abd	0.82 ± 0.04 a	1.27 ± 0.07 e	0.96 ± 0.01 A
Arctic Foothills	1.04 ± 0.03 ce	0.88 ± 0.04 bc	1.33 ± 0.08 f	1.03 ± 0.02 B
Coastal Plain	1.24 ± 0.10 bcef	1.08 ± 0.08 abc	1.53 ± 0.17 d	1.23 ± 0.10 B
Forage means	1.08 ± 0.03 A	0.91 ± 0.03 B	1.37 ± 0.10 C	
Gross energy (kJ/g DM) (n = 216)				
Brooks Range	18.6 ± 0.1 de	19.8 ± 0.1 g	17.6 ± 0.2 b	18.9 ± 0.1 A
Arctic Foothills	18.4 ± 0.1 cd	19.5 ± 0.2 fg	17.4 ± 0.2 ab	18.7 ± 0.1 AB
Coastal Plain	18.3 ± 0.1 c	19.4 ± 0.2 ef	17.2 ± 0.1 a	18.5 ± 0.1 B
Forage means	18.4 ± 0.1 A	19.6 ± 0.1 B	17.4 ± 0.2 C	
Digestibility (g/g DM) (n = 391)				
Brooks Range	0.487 ± 0.005 ab	0.635 ± 0.009 cd	0.830 ± 0.018 ef	0.587 ± 0.007 AB
Arctic Foothills	0.484 ± 0.005 a	0.634 ± 0.008 c	0.828 ± 0.012 e	0.585 ± 0.003 A
Coastal Plain	0.503 ± 0.006 b	0.652 ± 0.005 d	0.846 ± 0.015 f	0.604 ± 0.003 B
Forage mean	0.490 ± 0.004 A	0.639 ± 0.006 B	0.833 ± 0.014 C	
Digestible energy (kJ/g DM) (n = 297)				
Brooks Range	9.21 ± 0.05 a	12.42 ± 0.10 c	15.11 ± 0.44 e	10.80 ± 0.04 A
Arctic Foothills	8.86 ± 0.10 b	12.07 ± 0.10 d	14.76 ± 0.42 f	10.45 ± 0.07 B
Coastal Plain	9.07 ± 0.10 ab	12.29 ± 0.14 cd	14.98 ± 0.43 ef	10.66 ± 0.09 AB
Forage mean	9.00 ± 0.07 A	12.21 ± 0.09 B	14.91 ± 0.43 C	

Notes: Different lower case letters indicate significant pairwise differences ($P < 0.05$) among estimates for three ecoregions (rows) and three plant groups (columns) within each measure. Different upper case letters indicate significant differences among mean estimates among forage groups (within row) and ecoregions (within column), respectively.

threshold of 1% in browse at OD 187–198 (95% CI) and in graminoids at OD 203–214 (Fig. 3). Graminoids remained above 1% available N, but browse declined below that threshold at OD 229–237. The forb fell below the 1% N threshold for available and digestible fractions at ODs 191–232 (Fig. 3). Although total N concentration of forages was not significantly affected by ecoregion, both available and digestible fractions of N were greater on the Coastal Plain than the Brooks Range (Table 1). Total N and its fractions varied among years ($\chi^2 > 10.76$; 2 df; $P < 0.005$): Average values for 2011 were greater than those for 2013 for total N (2.11 ± 0.05 vs. 2.00 ± 0.05), available N (1.73 ± 0.05 vs. 1.55 ± 0.06), and digestible N (1.10 ± 0.03 vs. 0.97 ± 0.03).

Variation in digestible energy among years and ecoregions was less pronounced than that in digestible N. Predicted digestible energy content of forages was affected by year ($\chi^2 = 86.80$; 2 df;

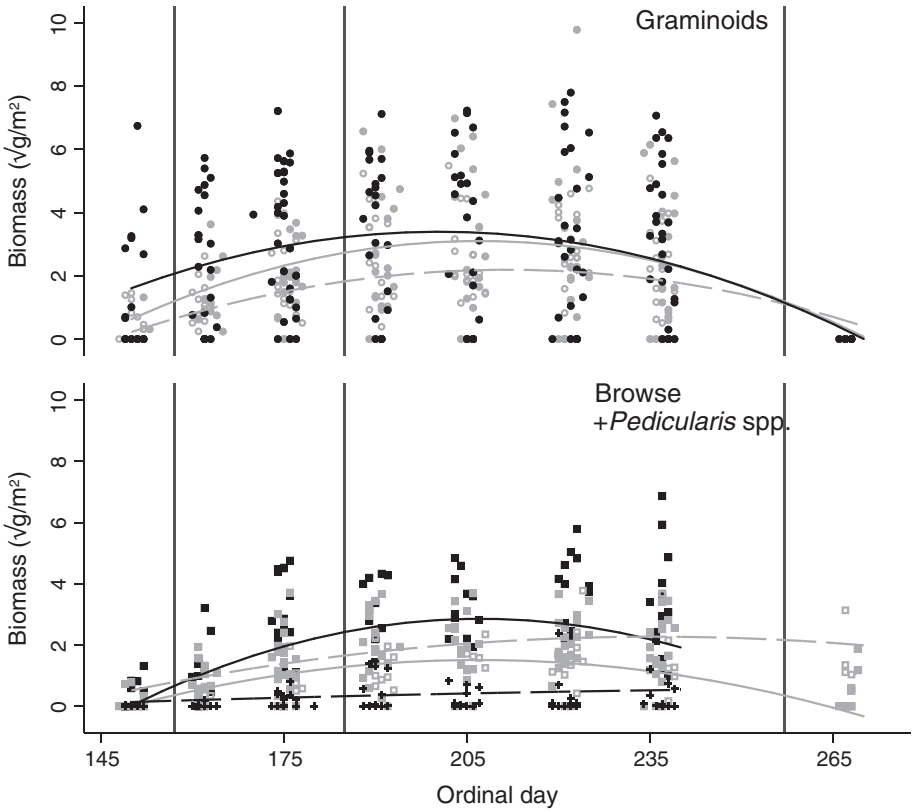

Fig. 2. Phenology of biomass ($\sqrt{g}/m^2$) in forages for Central Arctic Herd caribou. Vertical lines indicate average dates of parturition (157 d), early lactation (185 d), and weaning (257 d). Plots combine lines of predicted relationships from mixed-model regressions with observed data for each species. Graminoid plots include *Carex aquatilis* (solid gray circles with solid gray line), *Carex bigelowii* (open gray circles with dashed gray line), and *Eriophorum vaginatum* (solid black circles with solid black line). Browse plots include *Betula nana* (solid black squares with solid black line), *Salix pulchra* (solid gray squares with solid gray line), and *Salix richardsonii* (open gray squares with dashed gray line) with the forb *Pedicularis* spp. (+ symbols with dashed black line).

$P < 0.0001$), that is digestible energy contents in 2012 (10.99 ± 0.05 kJ/g) were greater than those in either 2011 (10.49 ± 0.09 kJ/g) or 2013 (10.20 ± 0.11 kJ/g). A similarly small significant change in digestible energy content (<0.5 kJ/g) was also predicted in comparisons of forages between the Brooks Range and the Arctic Foothills (Table 1). Differences in digestible energy content were much more pronounced in contrasts among plant groups that declined in increments of 2–3 kJ/g from the forb to the browse to graminoids (Table 1). Digestible energy declined over the summer in all forages species (Fig. 4), but only the digestible energy content of graminoids fell below the threshold of 9 kJ/g, which was estimated at ODs 221–232.

Anti-nutrients

Declines in digestible energy and digestible N were accompanied by a rise in the structural fiber content of both graminoids and browse species especially as plants began senescing at the end of the summer (Fig. 5). Although the range of observed ADF concentrations was similar between browse (0.23–0.50 g/g) and graminoids (0.16–0.53 g/g), total cell wall content was lower in browse (0.22–0.68 g/g) than graminoids (0.58–0.83 g/g) whereas lignin was greater in browse (0.07–0.37 g/g) than in graminoids (0.03–0.14 g/g; Appendix S1: Fig. S2). Concentrations of ADF in *Pedicularis* spp. rose and declined through the summer as the floral stalk developed and senesced to leave a basal cluster of stems with leaves at the

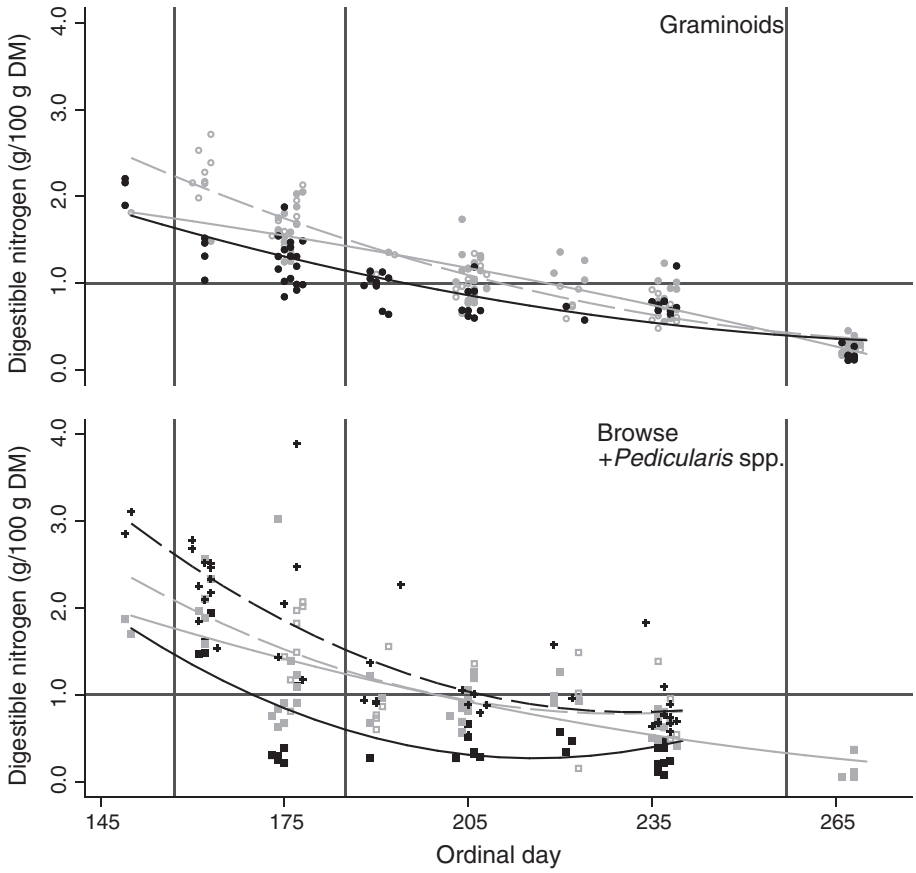

Fig. 3. Phenology of digestible N in forages for Central Arctic Herd caribou. Horizontal reference lines at 1 g N/100 g DM indicate a likely threshold of quality for protein gain in caribou cows and their calves. Vertical lines indicate average dates of parturition (157 d), early lactation (185 d), and weaning (257 d). Plots combine lines of predicted relationships from mixed-model regressions with the observed data for each species. Graminoid plots include *Carex aquatilis* (solid gray circles with solid gray line), *Carex bigelowii* (open gray circles with dashed gray line), and *Eriophorum vaginatum* (solid black circles with solid black line). Browse plots include *Betula nana* (solid black squares with solid black line), *Salix pulchra* (solid gray squares with solid gray line), and *Salix richardsonii* (open gray squares with dashed gray line) with the forb *Pedicularis* spp. (+ symbols with dashed black line).

end of summer (Fig. 5). Fiber contents in the forb were similar to those of browse species for ADF (0.15–0.40 g/g) and total cell walls (0.22–0.59 g/g), but lignin content was low and similar to that of graminoids (0.03–0.16 g/g; Appendix S1: Table S1, Fig. S2). Total cell walls were linearly related to ADF in browse ($Y = 0.12$ (± 0.03) + $X \cdot 1.11$ (± 0.09; 95% CI: 0.92–1.30); $n = 102$; $R^2 = 0.58$), graminoids ($Y = 0.42$ (± 0.01) + $X \cdot 0.81$ (± 0.05; 95% CI: 0.73–0.90); $n = 186$; $R^2 = 0.64$), and the forb ($Y = 0.09$ (± 0.02) + $X \cdot 1.29$ (± 0.08; 95% CI: 1.11–1.46); $n = 47$; $R^2 = 0.83$). Lignin was also linearly related to ADF in browse ($Y = X \cdot 0.67$ (± 0.04; 95% CI: 0.59–0.76); $n = 64$; $R^2 = 0.80$) and the forb ($Y = X \cdot 0.44$ (± 0.09; 95% CI: 0.26–0.62); $n = 23$; $R^2 = 0.54$), but this relationship between lignin and ADF was weak for graminoids ($Y = X \cdot 0.27$ (± 0.05; 95% CI: 0.17–0.36); $n = 90$; $R^2 = 0.25$).

Phenolic activity was consistently low in graminoids and the forb *Pedicularis* spp. (<11 mg/g; Appendix S1: Table S1). However, phenolic activity of browse species varied widely from low levels in *S. richardsonii* (8–6 mg/g) to a broad range of levels in *S. pulchra* (7–100 mg/g) that was associated with variation among years and within season (Appendix S1: Fig. S3). Phenols were negatively

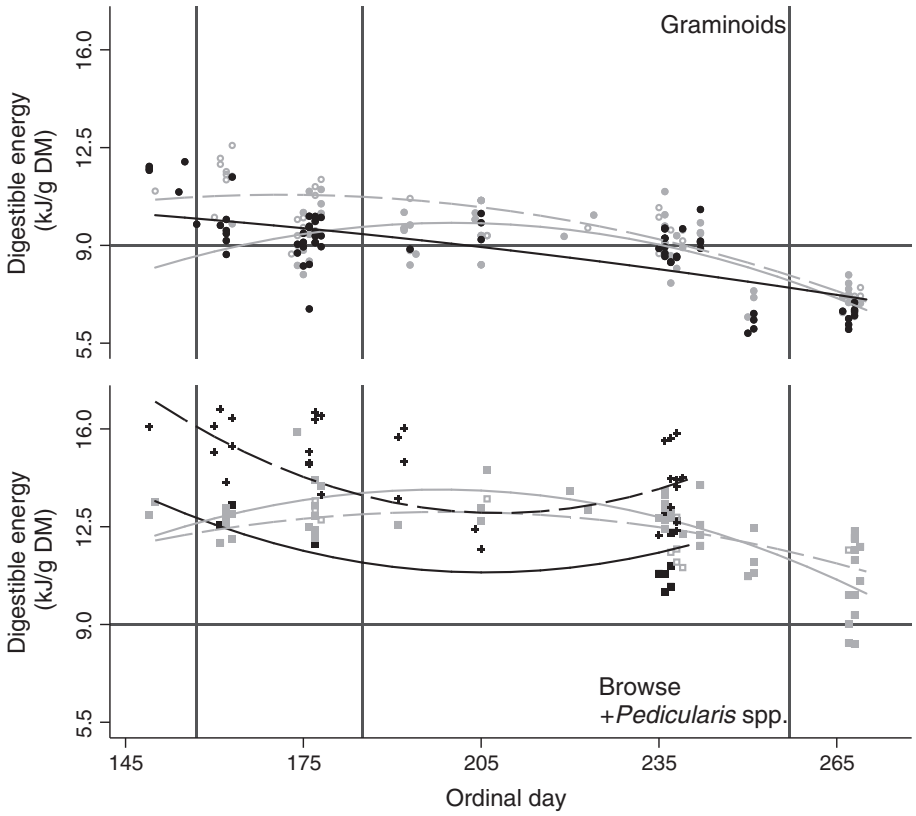

Fig. 4. Phenology of digestible energy (kJ/g DM) in forages for Central Arctic Herd caribou. Horizontal reference lines at 9.0 (kJ/g) indicate a likely threshold of quality for mass gain in caribou cows and their calves. Vertical lines indicate average dates of parturition (157 d), early lactation (185 d), and weaning (257 d). Plots combine lines of predicted relationships from the mixed-model regressions with the observed data for each species. Graminoid plots include *Carex aquatilis* (solid gray circles with solid gray line), *Carex bigelowii* (open gray circles with dashed gray line), and *Eriophorum vaginatum* (solid black circles with solid black line). Browse plots include *Betula nana* (solid black squares with solid black line), *Salix pulchra* (solid gray squares with solid gray line), and *Salix richardsonii* (open gray squares with dashed gray line) with the forb *Pedicularis* spp. (+ symbols with dashed black line).

associated with both digestible N (χ^2 = 4.71; 1 df; P = 0.03) and digestible energy (χ^2 = 7.31; 1 df; P = 0.001) in all three plant groups. An increase in phenolic content from 0 to 10 mg/g was associated with a reduction in digestible N content by 0.11 g/100 g and a reduction in digestible energy content by 0.11 kJ/g. However, effects of ADF on digestible N (χ^2 = 146.73; 1 df; P < 0.0001) and digestible energy (χ^2 = 211.32; 1 df; P < 0.0001) were more pronounced than those for phenols. An increase in ADF content from 0.25 to 0.35 g/g was associated with a reduction in digestible N content by 0.38 g/100 g browse, 0.97 g/100 g graminoid, and 0.56 g/100 g forb (Fig. 6). Similarly, an increase in ADF content from 0.25 to 0.35 g/g was associated with a reduction in digestible energy content by 1.44 kJ/g browse, 2.67 kJ/g graminoid, and 3.70 kJ/g forb (Fig. 6).

Discussion

Our hypothesis that N supply was more limiting than energy supply for caribou in summer was supported by comparisons of digestible N and energy contents with the respective threshold concentrations. Digestible energy content only fell below the limiting threshold (9 kJ/g) for graminoids after early lactation at 64–75 d from parturition (Fig. 4), whereas all forages fell below the limiting threshold for digestible N content (1%)

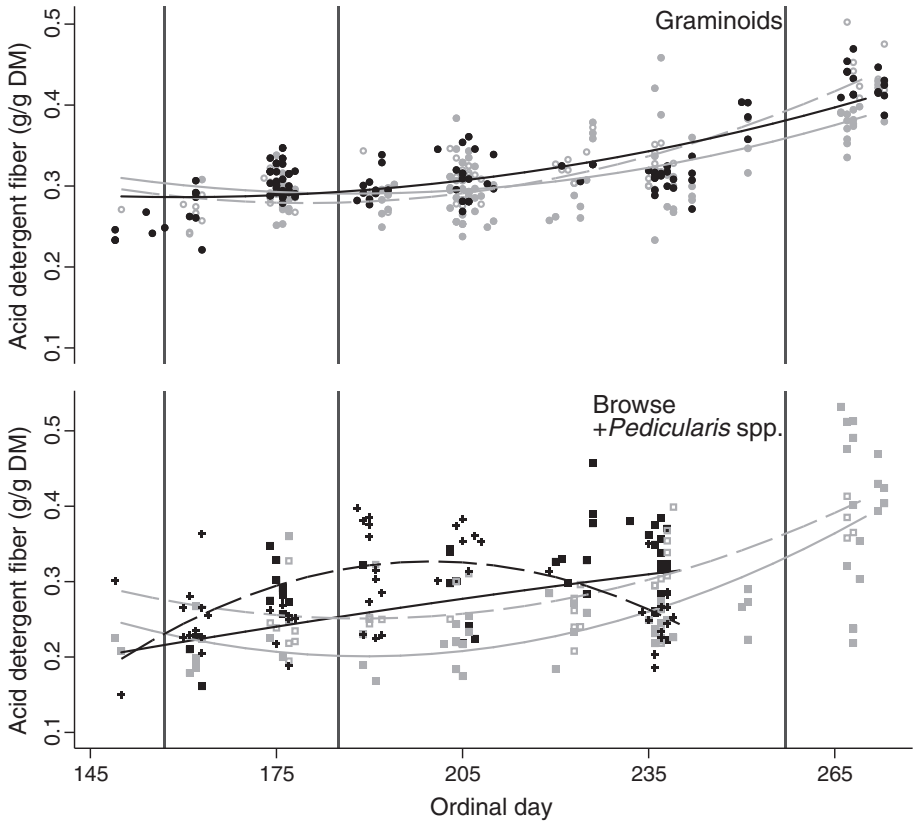

Fig. 5. Phenology of acid detergent fiber (g/g DM) in forages for Central Arctic Herd caribou. Vertical lines indicate average dates of parturition (157 d), early lactation (185 d), and weaning (257 d). Plots combine lines of predicted relationships from mixed-model regressions with the observed data points for each species. Graminoid plots include *Carex aquatilis* (solid gray circles with solid gray line), *Carex bigelowii* (open gray circles with dashed gray line), and *Eriophorum vaginatum* (solid black circles with solid black line). Browse plots include *Betula nana* (solid black squares with solid black line), *Salix pulchra* (solid gray squares with solid gray line), and *Salix richardsonii* (open gray squares with dashed gray line) with the forb *Pedicularis* spp. (+ symbols with dashed black line).

before female caribou would have weaned their calves at 100 d from parturition (Fig. 3). The window for digestible N was shortest for browse, which fell below the threshold of 1% soon after the period of early lactation at 30–41 d from parturition (Fig. 3), whereas digestible N contents of graminoids were adequate until 46–57 d and those from the forb were adequate until 34–75 d from parturition. The low quality of browse as a source of N was also apparent from concentrations of available N (i.e., the N not bound to fiber), which fell below the threshold of 1% albeit later in the season at 72–80 d from parturition.

Female caribou and their calves could select a mixture of graminoids, browse, and forbs to achieve adequate dietary concentrations of digestible energy and digestible N until 75 d post-parturition. Graminoids were the most abundant forage that accounted for 77% of the digestible N and 74% of the digestible energy in forage biomass above 1% N and 9 kJ/g in the first 75 d post-parturition. Low biomass and low mobility may limit forage selection to graminoids at parturition, but forage abundance increases through early lactation to peak at 50 d from parturition (Fig. 2) as female caribou and their calves increase their rates of movement and thus their ability to move among foraging areas (Fancy et al. 1989, Nicholson et al. 2016). Caribou are highly adaptive in their foraging behavior and can select for biomass as well as digestible contents of energy and nutrients especially when composition and density of

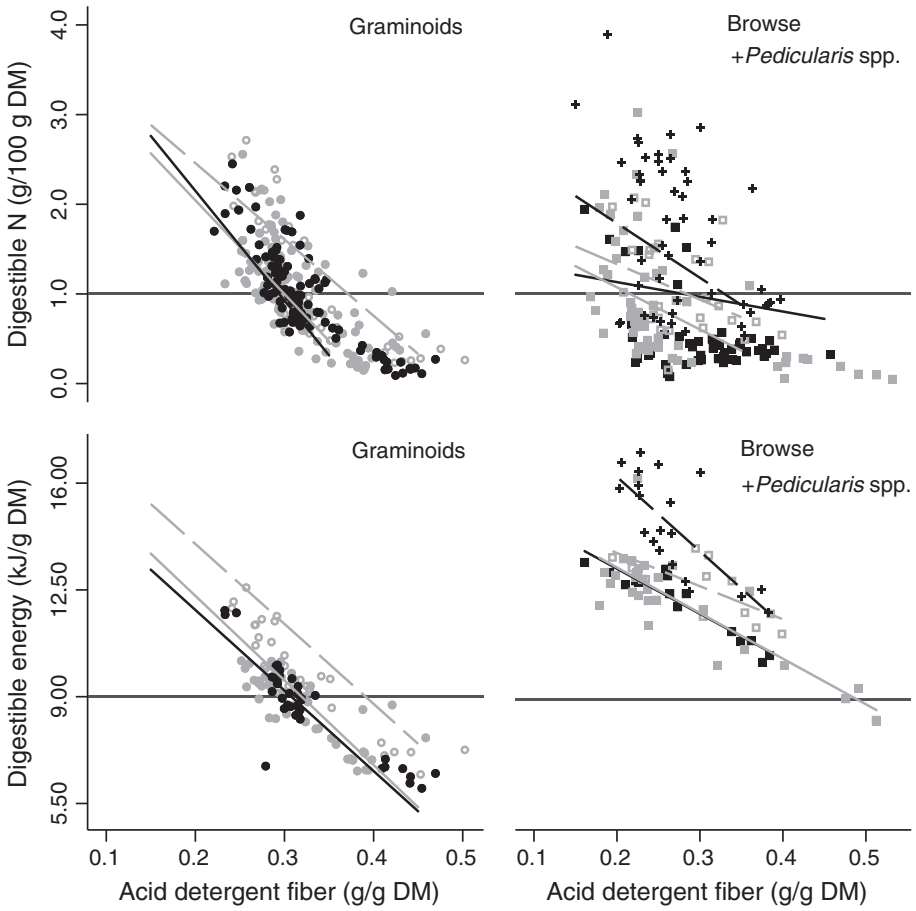

Fig. 6. Relationship between acid detergent fiber (g/g DM) and the content of digestible N (g/100 g DM) and digestible energy (kJ/g DM) in forages for Central Arctic Herd caribou. Horizontal reference lines at 1.0 g N/100 g DM and at 9.0 kJ/g indicate likely thresholds of quality for mass gain in caribou cows and their calves. Plots combine lines of predicted relationships from mixed-model regressions with the observed data points for each species. Graminoid plots include *Carex aquatilis* (solid gray circles with solid gray line), *Carex bigelowii* (open gray circles with dashed gray line), and *Eriophorum vaginatum* (solid black circles with solid black line). Browse plots include *Betula nana* (solid black squares with solid black line), *Salix pulchra* (solid gray squares with solid gray line), and *Salix richardsonii* (open gray squares with dashed gray line) with the forb *Pedicularis* spp. (+ symbols with dashed black line).

biomass are highly variable (van der Wal et al. 2000, Thompson et al. 2015, Denryter et al. 2017).

Forage selections are limited to senescing browse and graminoids in late summer when caribou are weaning their calves (Fig. 2). Late summer forages may support gains of body fat but not protein in caribou because the ratio of digestible N to digestible energy falls below the threshold for maximal microbial protein synthesis in the rumen (1.1–1.6 mg N/kJ; Nolan and Dobos 2005). Low ratios of digestible N to energy in browse may require N from the host usually in the form of secretions and recycled urea to sustain microbial fermentation and the digestion of carbohydrate (Barboza and Parker 2006). Low N to energy ratios can provide carbon for lipid synthesis or for oxidation but cannot provide enough N for a net gain in protein (Barboza et al. 2009). The low ratios of N to energy in late summer forages are consistent with a transition to the winter diet of lichens that are also low in N. Reindeer and caribou continue to use graminoids

in winter on islands where lichens have been removed by high densities of animals (Leader-Williams et al. 1981, Ricca et al. 2012, 2016).

Net gains in body protein may be delayed by the high demand for milk production; that is, female caribou may be unable to regain body stores of N until after early lactation at 28 d from parturition (Allaye Chan-McLeod et al. 1994, Barboza and Parker 2008). Consequently, the window for protein gain may be 28 d later and 28 d shorter than the time digestible N content is above the threshold of 1%, which is as little as 2 d for browse and 14 d for graminoids that first reach the threshold at 30 and 46 d from parturition, respectively. The Coastal Plain may be favored by female caribou because available and digestible concentrations of N are not only greater than those on the Brooks Range (Table 1), the window of usable N fractions is also delayed on the Coastal Plain. Digestible N concentration of graminoids on the Coastal Plain falls to the limiting threshold later than on the Brooks Range (41–48 vs. 47–76 d from parturition), which provides an average of 17 d longer for protein gain in females on the Coastal Plain. Caribou calves gain protein from birth, but most of that protein is from their mother as milk until the calves become more reliant on forage N after early lactation (Taillon et al. 2013). Areas with high digestible N after 4 July (OD 185) would be favorable for both the female caribou and her calf, which is supported by the positive relationship between calf survival and the biomass indexed by NDVI on 21 June in the calving area (Griffith et al. 2002). Adult male caribou can also regain protein stores from the start of spring, but those stores are used in rut soon after the end of summer (Barboza et al. 2004). Consequently, inland areas with greater biomass and densities of digestible N than the Coastal Plain may be more favorable for adult male caribou, which is consistent with spatial segregation of the sexes during the summer (Russell et al. 1993, Barboza and Bowyer 2001).

Variation in digestible energy and digestible N among years reflected changes in fiber (Fig. 6) and phenols (Appendix S1: Fig S3) that were probably associated with changes in growing conditions that altered the seasonal pulse of plant growth and thus the window for protein gain in caribou. Summer warming and early senescence in graminoids reduce digestible N and thus mass gains of domestic cattle and bison (*Bison bison*; Craine 2013, Craine et al. 2013). A decadal trend in warming is also associated with reduced N and increased fiber in the leaves of woody browse available to African primates (Rothman et al. 2015) that can result in body protein loss of individuals (Vogel et al. 2012). Primates and other herbivores may compensate for low concentrations of digestible N by increasing food intake even when intakes of energy and other nutrients exceed metabolic demands (Felton et al. 2009, Simpson et al. 2015). However, high fiber concentrations reduce the ability of animals to compensate for declines in digestible N or energy by increasing food intake especially in individuals of small body size like the calves of caribou (Barboza et al. 2009). The lignin in the fiber matrix contributes to the indigestible bulk of the forages but also serves as a plant secondary metabolite with phenolic components that impair supplies of digestible N and energy from woody browse. Seasonal changes in plant secondary metabolites such as tannins reduce digestible N of woody browse for moose and white-tailed deer (*Odocoileus virginianus*) that likewise impair protein gains (McArt et al. 2009, Windels and Hewitt 2011). Although caribou and reindeer can tolerate fiber and some plant secondary metabolites, the dynamic nature of these anti-nutrients probably contributes to variability in forage selection among populations. For example, the low digestible N content of the birch *B. nana* is related to its high content of lignin and phenols that likely limits the use of this species by caribou in Alaska (Kuropat 1984) even though a closely related species of birch (*B. glandulosa*) is used by caribou in Quebec (Manseau et al. 1996) and can be consumed by caribou in Alaska (Thompson and Barboza 2014).

Our study provides evidence that digestible N is more limiting than digestible energy for caribou and that phenological windows for protein gain in caribou vary with ecoregion and year, which is likely to affect the distribution and growth of the population. Our combination of in vitro digestion and detergent extraction can be used to monitor N in forages at focal areas of the calving range and in areas used by caribou after early lactation to assess the annual window of protein gain for caribou. The relationships we provide for ADF in woody browse and graminoids can also be used

to predict cell wall contents and lignin to assess the effects of summer warming on maturation of forages that are likely to affect food intake and the window for protein gain in caribou. Complimentary measures of forage quality and the condition of calves at the end of summer may provide metrics for predicting the trajectory of populations especially when numbers decline to levels that impact both social and ecological systems (Nicolson et al. 2013).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2073/full