# Early fall and late winter diets of migratory caribou in northwest Alaska

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*Abstract:* Lichens are the primary winter forage for large herds of migratory caribou (*Rangifer tarandus*). Caribou select for lichens more than they are available across the landscape and they generally avoid, during winter, habitat that has been burned by wildfires for decades while lichen abundance recovers. However, the relative importance of lichens in the diet is subject to debate. From 2010-2013, we conducted one of the largest microhistological studies of the early fall (58 samples from 1 site) and late winter (338 samples from 58 sites) diets of barren-ground caribou. Lichens constituted ~ 71% of the late winter diets of caribou in northwest Alaska, whereas moss (11%) and shrubs (9%) were the next most common forage items. Early fall diets were very similar to late winter, perhaps because deciduous vegetation is senescent during both periods. Diets of males, non-pregnant females and pregnant females were not significantly different. Pregnancy was not associated with the abundance of any forage type during winter, but was associated with higher physiological stress. This result was expected as fall body condition dictates conception, caribou are 'capital' breeders, and gestation can be energetically demanding. Caribou that migrated south (i.e., wintered south of 67.1°N) had lower levels of nutritional stress, higher levels of lichen in the diet, and lower levels of moss and shrubs compared to caribou that did not migrate south. Future investigations into the potential connection between lichen abundance in the winter diet and survivorship, as well as linking the late summer diets of individuals to their reproductive success, should be undertaken.

**Key words:** body condition; lichens; migration; moss; nutrition; pregnancy; *Rangifer tarandus granti*; stress.

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## Introduction

The importance of lichens in the winter diet of caribou (*Rangifer tarandus*) has been debated for nearly a century (Klein, 1982). Terricolous lichens constitute the majority of the diet of migratory barren-ground caribou that face predation pressure (Klein, 1982; Russell *et al.*, 1993; Joly *et al.*, 2007b; Gustine *et al.*, 2012; Joly *et al.*, 2015). However, non-migratory populations exist with little to no lichen in their diet (Thomas & Edmonds, 1983; Adamczewski *et al.*, 1988). These populations often experience little to no predation pressure. Migration and predator avoidance behavior both require additional energetic expenditures; expenditures that may be filled by lichen consumption during winter months.

Pregnancy is largely determined by body condition in the fall (Cameron *et al.*, 1993; Cameron & ver Hoef, 1994; Gerhart *et al.*, 1997). Maternal investment in the fetus is relatively small for caribou during the first 2 trimesters (i.e., winter), with approximately 84% of the protein allocation deriving from endogenous sources stored during early winter (Barboza & Parker, 2008). With minimal early maternal investment, fetal resorption is uncommon (Thomas & Barry, 1990). Nitrogen (N) demands peak again during lactation, which occurs in late May and early June (Barboza & Parker, 2008). The abundance of lichen, or any other forage class, in the winter diet should not be strongly linked with pregnancy, parturition or lactation as caribou are 'capital' breeders (Barboza & Parker, 2008; Taillon *et al.*, 2013; Gustine *et al.*, 2017). Capital breeders rely heavily on stored resources to supply fetal development and milk production, in contrast to 'income' breeders which utilize contemporaneous forage intake for these processes.

The amount of lichens in the diets of migratory caribou far exceeds their relative abundance on the landscape (Joly *et al.*, 2007b). Because lichens are so prevalent in the diet and caribou actively select for them, declines in lichen abundance are a concern for caribou management and conservation. Shrubification of the Arctic, overgrazing, and changing climatic conditions are thought to be detrimental to lichens (see review by Joly *et al.*, 2009). Wildfires, which consume caribou forage lichens, are predicted to increase (Joly *et al.*, 2012) in the rapidly warming climate of the Arctic (Comiso & Hall, 2014). Adding concern about the abundance of lichens on the landscape are the effects of proposed and existing industrial development (e.g. Wilson *et al.*, 2013; Wilson *et al.*, 2014; Wilson *et al.*, 2016). In the Arctic, dirt is often the surface of industrial roads and road dust that traffic creates can reduce lichen cover (Exponent, 2007; Chen *et al.*, 2017). In response to lingering questions about the importance of lichens in the diet of overwintering, migratory caribou that face predation pressure in relation to pregnancy, parturition, and sexual segregation, as well as a desire to possess baseline data prior to additional industrial development, we analyzed fall and early winter diets. Specifically, we wanted to test 1) if lichens were a critical component of the diet of caribou in the region, 2) that late winter diet was not related to pregnancy status, 3) if there were differences in the diets of pregnant females, non-pregnant females, and males, and 4) if fall diets at Onion Portage varied annually.

## Material and methods

### *Study area*

The study area included most of the annual range of the Western Arctic Herd, covering over 360,000 km$^2$ (Fig. 1; Joly *et al.*, 2007a). This vast region encompasses coastal to continental climates of the arctic and subarctic with expanses of tundra, boreal forest, wetlands and mountains. See Joly *et al.*, (2007a; 2010) for more details about the study area. The size of the Western Arctic Herd oscillated from a low of about 75,000 in 1976 to maximum of nearly 500,000 caribou in 2003 and declined to 201,000 in 2016 (ADFG, 2011; Joly *et al.*, 2011; ADFG, 2016.). Teshekpuk Lake Herd and Central Arctic Herd caribou can be sympatric with the Western Arctic Herd during winter (ADFG, 2011; Person *et al.*, 2007). Therefore, all samples were designated 'arctic' caribou rather than being parsed by herd (see Joly *et al.*, 2015).

Average temperatures for September of 2010-2012 were about average (5°C) for each year. September 2010 was very dry, 2011 normal and 2012 set records for amount precipitation. Late winter 2011 had normal temperatures (-16°C), but rain-on-snow events in locations occurred earlier in the winter in parts of the study area. In 2012, late winter was colder than normal and had deep snow. Late winter of 2013 was characterized by cool temperatures and low snow accumulation (National Weather Service data available online at http://w2.weather.gov/climate/index.php?wfo=pafc).

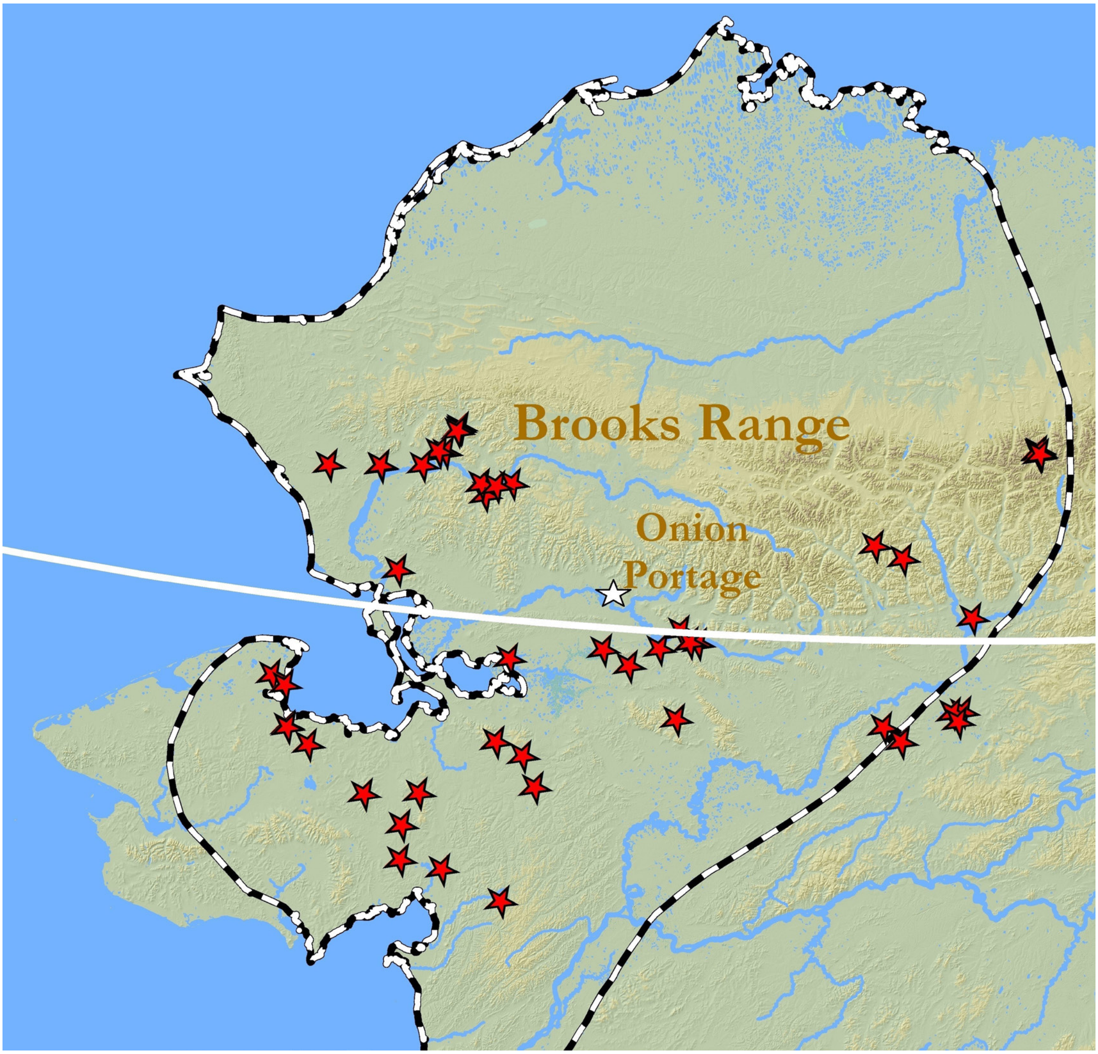

Figure 1. Study area map indicating the locations of fecal sample collection sites in northwest Alaska, 2010-2013. Red stars indicate late winter sites and the white star is Onion Portage where all early fall collections were made. The black and white dashed line indicates the approximate boundary of the Western Arctic Herd's range (courtesy of the Alaska Department of Fish and Game). The white line indicates 67.1°N.

*Fecal pellet collection*

All fall ($n = 58$) fecal samples were collected at Onion Portage, Kobuk Valley National Park (Fig. 1) during the month of September, 2010-2012. We collected a total of 338 samples during late winter; 19 samples from 2 sites from April 15-27, 2011, 188 samples from 38 sites from February 7 to April 27, 2012, and 131 samples from 18 sites from April 15-17, 2013. Locations were primarily accessed by small ski-equipped planes (*e.g.*, Piper PA-18 Super Cub), though some were reached by dog team or snowmachine. We collected 10 to 15 fresh pellets from isolated groupings, both in fall and late winter, and stored them frozen in plastic bags until analyses were conducted. The mean number of samples per location was 6 (range 1-16). We avoided the smaller pellets typical of calves.

### *Microhistological and hormone analyses*

All 396 samples collected were sent in for microhistological diet analysis. Microhistological results for the 188 samples collected during the winter of 2012 were previously reported by Joly *et al.* (2015). We had all of the samples analyzed at the same laboratory to minimize sources of error (see Russell *et al.*, 1993). Relative density of plant fragments was based on 100 views per sample (Level B). We then corrected these results for apparent digestibility following the methodology of Boertje (1984) and Gustine *et al.* (2011).

Late winter samples from 2012 and 2013 were subjected to hormonal analysis and definitive sex determinations were made for 297 of 319 samples (previously reported in Joly *et al.,* 2015); none of the fall samples or the 2011 late winter samples were similarly analyzed. Pregnancy and levels of glucocorticoid (cortisol), and the thyroid hormone triiodothryronine (T3) were also determined (Joly *et al.*, 2015). Analytical methods and results were detailed by Joly *et al.* (2015). Joly *et al.* (2015) identified 67.1°N as a line roughly separating caribou wintering in their traditional, southern core area and those in the more mountainous north that is used by far fewer individuals.

### *Statistical analyses*

For the fall data, we employed analysis of variance (ANOVA) for diet comparisons among years since all samples were collected at the same location and hormone analyses were not performed. Significance was defined at $\alpha = 0.05$ level. For winter data collected in 2012 and 2013, we used linear mixed-effects models to test for relationships for each dietary class and the predictors of pregnancy/sex class (i.e., non-pregnant female, pregnant female, male), winter range (i.e., north or south), cortisol levels, T3 levels, year, and timing in winter (day of year). Site was included as a random effect and we excluded data from 2011 because hormone analyses were not conducted for samples from that year. We used the same procedure to test for differences in cortisol and T3 levels across sex/pregnancy categories, winter ranges, years, and timing in winter. We logit transformed the proportional data for each of the 5 diet categories (Warton & Hui, 2011). We employed a top-down model building strategy to identify significant predictors for each diet category and hormone level following the methods outlined in Zuur *et al.* (2009) and reported results from the most parsimonious model. We used likelihood ratio tests to test for significance of predictor variables and performed all analyses in R 3.3.3 (R Core Team, 2017) using the 'lme4' package (1.1-12, Bates *et al.*, 2015) for model fitting, the 'car' package (2.1-6, Fox & Weisberg, 2011) for data transformation, and the 'MuMIn' package (1.15.6, Bartoń, 2016) to calculate conditional $R^2$.

## Results

### *Fall data*

Lichens dominated the early fall diet of adult caribou, comprising 65.9 ± 1.3% (3-year mean and SE) of their forage intake (Fig. 2). Shrubs and moss were the next most common forage classes but only represented 11.3 ± 1.0% and 8.1 ± 0.5% of the diet, respectively. There was limited inter-annual variability (Fig. 2): mushrooms were a significantly ($F_{2,55} = 58.96$, $P < 0.01$) greater proportion of diet in 2010 (11.0 ± 0.8%) than 2011 or 2012 (none in either year), mosses were a significantly ($F_{2,55} = 20.04$, $P < 0.001$) greater proportion of diet in 2011 (11.7 ± 0.7%) than 2010 (5.8 ± 0.6%) or 2012 (7.7 ± 0.8%), and shrubs were significantly ($F_{2,55} = 4.92$, $P = 0.011$) more common in 2011 (15.1 ± 1.8%) than 2010 (8.1 ± 1.5%), but not 2012 (12.2 ± 1.8%). Lichens, forbs and graminoids

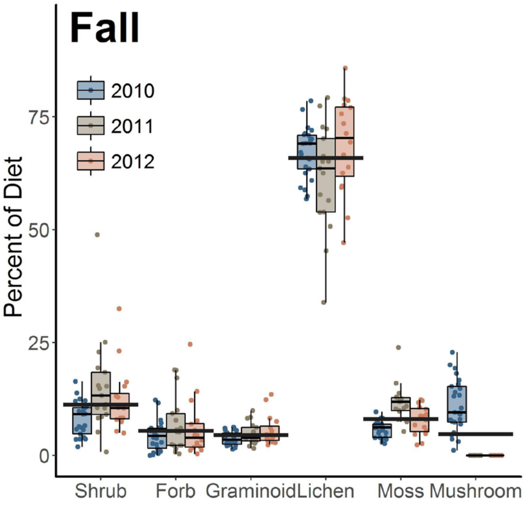

Figure 2. Early fall (September) diets of adult caribou from Onion Portage, Kobuk Valley National Park, northwest Alaska, 2010-2012. The thin bar inside the boxplots represents the median. The thick bar spanning all 3 years represents the 3-year mean.

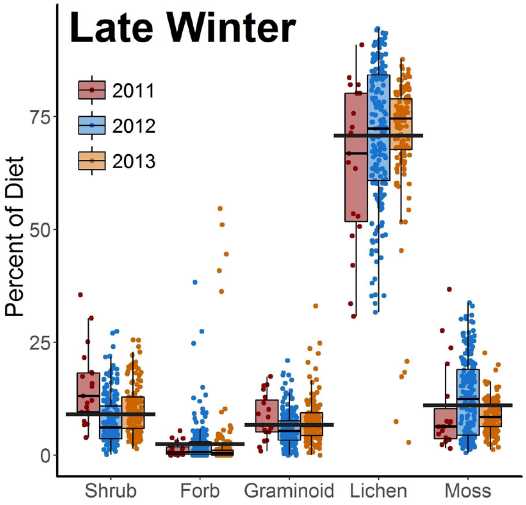

Figure 3. Late winter diets (February-April) of adult caribou in northwest Alaska, 2011-2013. The thin bar inside the boxplots represents the median. The thick bar spanning all 3 years represents the 3-year mean.

exhibited no significant differences among the 3 years of sampling.

*Winter data*

Overall (2011-2013, *n* = 338), lichens dominated the diet of adult caribou in winter as well, comprising 70.8 ± 0.8% (3-year mean and SE) of their forage intake (Fig. 3). For the 2012-2013 data, we found significant differences in the percentage of lichens in the diet between winter ranges ($\chi^2$ (1) = 12.53, $P < 0.01$); diets of caribou on the southern winter range had a greater percentage of lichens in their diets than caribou on the northern winter range (Fig. 4A, $\hat{\beta}_{\text{South}}$ = 0.605 ± 0.184 SE, logit space). All sites (*n* = 9) with an average of < 59% lichens in the diet were on the northern winter range, while all sites (*n* = 15) with > 80% were in the south. Lichens were significantly positively related to cortisol ($\chi^2$ (1) = 6.53, $P = 0.01$); greater lichen percentages were associated with higher cortisol levels ($\hat{\beta}_{\text{Cortisol}}$ = 0.004 ± 0.001 per unit cortisol, logit space), as well as a significant negative relationship to timing in winter ($\chi^2$ (1) = 5.54, $P = 0.02$); less lichens were in the diet as winter progressed ($\hat{\beta}_{\text{Timing}}$ = -0.022 ± 0.006, logit space). While Joly *et al.* (2015) noted that consumption of lichens by pregnant females was significantly less than either non-pregnant females or males in 2012, with the addition of 2013 data we detected no significant relationships in the percentage of lichens among sex/pregnancy categories ($\chi^2$ (1) = 3.50, $P = 0.17$). We found no significant differences in the proportion of lichens in the diet across years or T3 levels. Conditional $R^2$ of the top performing model (lichens ~ winter range + cortisol levels + winter timing) was 80.3%.

Moss was the next most common forage class, but represented only 11.0 ± 0.4% of the diet (3-year mean and SE, Fig. 3). For the 2012-2013 data, percentage of moss in the diet varied significantly between winter ranges ($\chi^2$ (1) = 12.25, $P < 0.01$); diets of caribou in the south contained less moss than caribou in the

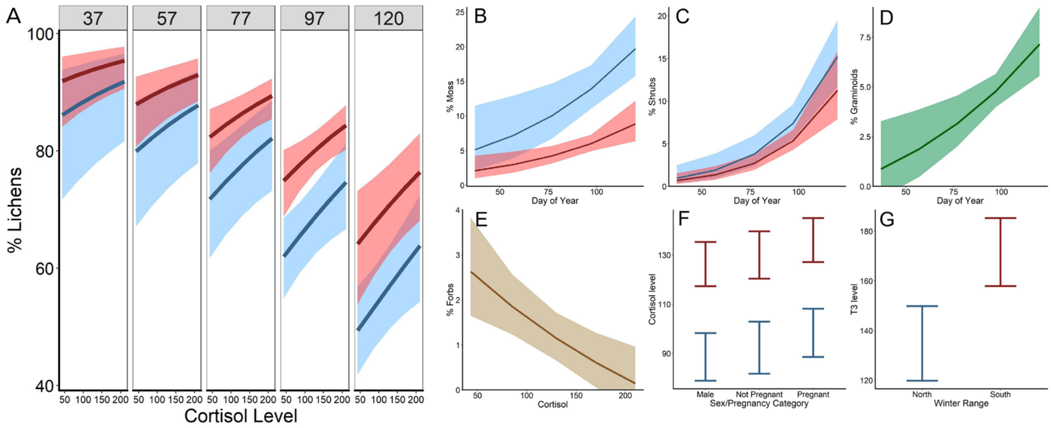

Figure 4. Predicted results from top fitted models in the analysis of winter diet data for caribou in northwest Alaska 2012-2013. Plots are the fitted results from the best performing model for lichen (A), moss (B), shrubs (C), graminiods (D), forbs (E), cortisol level (F) and T3 level (G). When the winter range category was significant, red-shaded lines represent the southern range (south of 67. 1°N) and blue-shaded lines depict the northern range. Bands (A-E) and bars (F and G) depict 95% confidence intervals. For percent lichen (A), sub-plots depict the specified day of year, indicated at the top of each plot.

north (Fig. 4B, $\hat{\beta}_{South}$ = -0.928 ± 0.173, logit space). Caribou on the northern winter range had more than double the amount of moss in their diet (16.4 ± 0.5%) than caribou in the south (7.7 ± 0.4%, 2-year means). Additionally, percentage of moss in the diet increased significantly ($\chi^2(1) = 8.64$, $P < 0.01$) as winter progressed ($\hat{\beta}_{Timing}$ = 0.018 ± 0.006 per day, logit space). Percentage of moss did not significantly differ across years, sex/pregnancy categories, or cortisol and T3 levels. Conditional $R^2$ of the top performing model (moss ~ winter range + winter timing) was 77.0%.

Shrubs were the next most common forage class after mosses and represented 9.1 ± 0.3% of the diet (3-year mean and SE, Fig. 3). For the 2012-2013 data, percentage of shrubs in the winter diet varied significantly between northern and southern ranges ($\chi^2$ (1) = 5.22, $P$ = 0.02) and exhibited a significant positive relationship with winter timing ($\chi^2$ (1) = 13.46, $P < 0.01$). Diets of caribou residing in the south contained less shrubs than diets of caribou residing in the northern range (Figure 4C, $\hat{\beta}_{South}$ = -0.346 ± 0.189, logit space). Caribou on the northern winter range had 50% more shrubs in their diet (11.0 ± 0.5%) than those in the south (7.3 ± 0.4%, 2-year means). The percentage of shrubs in caribou diets increased as winter progressed ($\hat{\beta}_{Timing}$ = 0.035 ± 0.007 per day, logit space) in both the northern and southern winter ranges. Percentages of shrubs did not significantly differ between years, sex/pregnancy categories, or either hormone levels. Conditional $R^2$ of the top performing model (shrubs ~ winter range + winter timing) was 67.6%.

Graminoids comprised 6.7 ± 0.3% of caribou diets (3-year mean and SE, Fig. 3). For the 2012-2013 data, percentage of graminoids significantly varied with timing in winter ($\chi^2$ (1) = 6.29, $P$ = 0.01); greater proportions of graminoids occurred in the diet as winter progressed (Fig. 4D, $\hat{\beta}_{Timing}$ = 0.013 ± 0.004 per day, logit space). We found no significant relationship across years, between sex/pregnancy categories, winter range, or either hormone level for graminoids. Conditional $R^2$ of the top model (graminoids ~ winter timing) was 59.9%.

Forbs (6.0 ± 0.4%) comprised the smallest proportion of caribou diet classes (3-year mean and SE, Fig. 3). For the 2012-2013 data, percentage of forbs in the diet exhibited a significant negative relationship with cortisol levels ($\chi^2$ (1) = 6.42, $P = 0.01$); percent of forbs decreased with higher levels of cortisol (Figure 4E, $\hat{\beta}_{\text{Cortisol}} = -0.004 \pm 0.001$ per unit cortisol, logit space). We found no significant difference across years, between sex/pregnancy categories, wintering range, T3 levels, or winter timing for percentage of forbs. Conditional $R^2$ of the top model (forbs ~ cortisol levels) was 61.5%.

Winter range exhibited a significant effect on both cortisol level ($\chi^2$ (1) = 15.92, $P < 0.01$) and T3 level ($\chi^2$ (1) = 10.68, $P < 0.01$). Additionally, cortisol levels significantly varied among sex and pregnancy classes ($\chi^2$ (1) = 13.98, $P < 0.01$). Cortisol levels were highest for pregnant females (9.8 ± 2.7 greater than males, Fig. 4F), followed by non-pregnant females (3.7 ± 3.3 greater than males), and lowest for males (88.6 ± 4.9), while caribou in the southern range had higher cortisol levels for all 3 categories (37.7 ± 6.4 greater for each category). T3 levels were lower for caribou in the northern range (134.8 ± 7.6, Fig. 4G) than for caribou in the southern range (171.6 ± 7.0). Conditional $R^2$ of the top models were 72.7% (cortisol ~ sex/pregnancy category + winter range) and 72.1% (T3 level ~ winter range). The proportion of females that were pregnant was not significantly different between northern (70.3 ± 5.4%) and southern (69.7 ± 4.4%) sites.

## Discussion

This study (which includes data presented by Joly *et al.* (2015)) is one of the most extensive microhistological analyses of caribou diets to date. In concurrence with other studies (e.g., Boertje, 1984; Boertje, 1990; Saperstein, 1996; Joly *et al.*, 2007b; Gustine *et al.*, 2012), we found that lichens constituted the majority of the diet for most caribou, with some (~ 6%) individuals having more than 90% in their diet. For the past 40 years, lichens have typically comprised 65 - 70% of the diet of migratory caribou that face substantive predation pressure (Table 1). Lichens are consumed far more than their relative availability on the landscape (Joly *et al.*, 2007b). Caribou that persist at low densities, do not migrate, face reduced predation pressure, and have smaller body sizes are known to survive with limited lichen consumption (Thomas & Edmonds, 1983; Adamczewski et al., 1988). The question of why large migratory herds of caribou utilize lichens so heavily remains.

The amount of lichen, or any other dietary component, in the late winter diet of caribou was not associated with females being pregnant (Joly et *al.*, 2015; *this study*). Pregnancy is determined in the fall and is associated with body condition, often indexed by mass, at this time (Cameron *et al.*, 1993; Cameron & ver Hoef, 1994; Gerhart *et al.*, 1997). Caribou rely heavily on stored resources for their investment in fetal development and early lactation (i.e., they are 'capital' breeders; Barboza & Parker, 2008; Taillon *et al.*, 2013; Gustine *et al.*, 2017). These resources are typically accumulated prior to vegetative senescence and shortly thereafter. Thus, the importance of lichens does not appear to be linked with pregnancy, parturition or early lactation.

Indices of higher nutritional stress (i.e., low T3 levels) were greater for caribou on their northern winter range as compared to the southern winter range. There was more than 2 times the proportion of moss and 50% more shrubs in the diets of caribou on the northern winter range. Moss and shrubs account for the discrepancy in the levels of lichens reported in their diets on their northern and southern winter ranges. There were ~ 25% fewer lichens in the diets of caribou at these northern locations, which is in concurrence with other studies (Ta-

Table 1. Percentage of lichens in the late winter diet of 'arctic' caribou reported from other projects. WAH is Western Arctic Herd, TCH is Teshekpuk Caribou Herd, CAH is Central Arctic Herd, and PCH is Porcupine Caribou Herd.

| Age/Sex Class | Herd(s) | N | Lichens % | Year(s) | Study |
|---|---|---|---|---|---|
| All classes | WAH, TCH | 3 | 60 | 2008 | Gustine *et al*., 2012 |
| All classes | WAH, TCH | 6 | 77 | 2007 | Gustine *et al*., 2012 |
| All classes | WAH, TCH | 5 | 68 | 2006 | Gustine *et al*., 2012 |
| Adults | WAH, TCH | 23 | 64 | 2005 | Joly *et al*., 2007b |
| Adults | WAH, TCH | 23 | 72 | 1995-96 | Joly *et al*., 2007b |
| All classes | WAH, TCH | | 59[a] | 1991 | Saperstein 1966 |
| All classes | WAH, TCH | | 74[a] | 1990 | Saperstein 1996 |
| All classes | TCH | 2 | 28 | 2004 | Parrett 2007 |
| All classes | CAH | 3 | 47 | 2008 | Gustine *et al*., 2012 |
| All classes | CAH | 4 | 61 | 2007 | Gustine *et al*., 2012 |
| All classes | CAH | 4 | 76 | 2006 | Gustine *et al*., 2012 |
| All classes | PCH | 15 | 67 | 1979-82 | Russell *et al.* 1993 |
| All classes | PCH | 100 | 67 | 1973 | Thompson & McCourt 1982 |

[a] Unknown if value corrected for apparent digestibility.

ble 1). These northern sites also have a lower predicted probability of use as determined by resource selection function (RSF) models (Joly, 2011). Pregnancy rates were greater at the northern sites, but not significantly so. Higher levels of cortisol were correlated with being pregnant. Indications of physiological stress (i.e., high cortisol levels; see Morton *et al*., 1995; Dehnhard *et al*., 2001; Möstl & Palme 2002) were low for caribou at the northern sites (*this study*) and highest at mid-latitudes (Joly *et al*., 2015). We posit that some migratory caribou enter winter in good enough condition that they do not migrate to their traditional winter grounds and, instead, spend winter on inferior range. The potential benefits of such behavior are reduced energetic expenditure for locomotion and reduced exposure to predation along the migration route. While robust data is currently lacking, adult survivorship appears to be lower at these northern sites (Joly *et al*., 2015). Hence, abundance of lichens in the winter diet may be linked to adult survivorship (Joly et *al*., 2015), but this hypothesis remains untested. Lower population densities and physiological differences dictated by smaller body size are other potential key, and not necessarily mutually exclusive, factors that could allow some caribou populations to persist without lichens.

In contrast to Joly *et al.* (2015), we found no significant differences in the amount of lichens, or any other forage class, among pregnant females, non-pregnant females and males. Sexual segregation is common in caribou during winter (Cameron & Whitten, 1979; Jakimchuk *et al*., 1987), though it was muted in northwest Alaska (Joly *et al*., 2015). The apparent lack of dietary niche separation during this time suggests behavioral rather than physiological or nutritional differences drive segregation. Males appear to utilize rougher terrain that suggests a risk-adverse, energy conservation strategy versus females that may utilize habitats with greater lichen availability to maximize energy intake but also increase predation exposure (Joly, 2011). Increased exposure could be mitigated by females forming larger groups (Roberts, 1996). Utilization of lichen starts to decline in late winter (Russell *et al.*, 1993; Joly *et al.*, 2015, *this study*), while graminoid usage increases (*this study*). This change in diet may reflect the increasing availability of other forage items as snow melts, increasing need for protein, or both (Joly *et al.*, 2015).

Most deciduous vegetation has senesced by early fall in the Arctic and northern sub-arctic. In agreement with previous studies (Thompson & McCourt, 1981; Russell *et al.*, 1993; Parrett, 2007), we found that early fall diets were very similar to late winter diets (Figs. 2 & 3). Given that most deciduous vegetation has senesced during both of these time frames, this result should not be surprising. This adds support to the hypothesis that late summer (after peak insect harassment but before vegetative senescence) is a critical foraging window for caribou to gain the requisite resources to become pregnant, calve, and endure early lactation requirements for females and for males to endure the rigors of the rut (see Joly *et al.*, 2011; Joly *et al.*, 2015; Gustine *et al.*, 2017).

## Conclusions

For at least 4 decades, research has consistently documented lichens as being the most abundant forage item in the winter diets of migratory caribou; however, that abundance of lichens is not related to pregnancy rate. Lichens are highly digestible and high in carbohydrates (Person *et al.*, 1980). This makes lichens a good source of energy for caribou, perhaps facilitating overwinter survival. Future research should examine the potential nexus between lichens in the diet and survivorship during winter. Additionally, researchers should investigate links between diets of specific individuals to their reproductive performance and survivorship, especially during the late summer foraging window.

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