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What do caribou eat? A review of the literature on caribou diet

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Abstract

Historically the study of diet caribou and reindeer (*Rangifer tarandus* (Gmelin, 1788)) has been specific to herds and few comprehensive circumpolar analyses of *Rangifer* diet exist. As a result, the importance of certain diet items may play an outsized role in the caribou diet zeitgeist, e.g., lichen. It is incumbent to challenge this notion and test the relevant importance of various diet items within the context of prevailing hypotheses. We provide a systematic overview of 30 caribou studies reporting caribou diet and test biologically relevant hypotheses about spatial and temporal dietary variation. Our results indicate that in the winter caribou primarily consume lichen, but in warmer seasons, and primary productivity is lower, caribou primarily consume graminoids and other vascular plants. In more productive environments, where caribou have more competitors and predators, consumption of lichen increased. Overall, our description of caribou diet reveals that caribou diet is highly variable, but in circumstances where they can consume vascular plants, they will. As climate change affects Boreal and Arctic ecosystems, the type and volume of food consumed by caribou has become an increasingly important focus for conservation and management of caribou.

Keywords: Caribou conservation, dietary niche, lichen, niche variation, *Rangifer*

Open access data: all code and data used for analyses are available at:

<https://gitlab.com/qwebber/caribou-foraging>

32 Introduction

33 Species with a circumpolar biogeography occupy regions that vary markedly in the local
34 availability of resources. As such, individuals, populations, or species can exhibit variation in
35 their resource use, a specialization termed niche variation (Van Valen 1965). Dietary niche
36 variation between species is a common phenomenon among northern species, allowing for
37 coexistence in regions with limited food resources (Bolnick et al. 2003; Maldonado et al. 2019).
38 Yet even in systems with low species richness, e.g., Boreal and Arctic ecosystems, the plants on
39 which herbivores rely differ in their composition and abundance (White 1983), suggesting that
40 similar intra-specific variation in diet should also exist. Several key variables can influence the
41 dietary niche of an individual, population, or species, depending on the scale at which they are
42 applied. For example, spatial variation in biological interactions, including predation, parasitism,
43 and competition, can influence dietary variation between populations within a species. However,
44 local variation in these same factors could apply more specifically to individuals within a
45 population, leading to individual variation in dietary niches. Spatiotemporal variation in the
46 availability of resources and competition for available resources can also result in variation in the
47 dietary niche for species typically considered specialists (Bolnick et al. 2003; Maldonado et al.
48 2019). *Rangifer tarandus* (Gmelin, 1788), i.e., caribou and reindeer (hereafter, caribou), are a
49 circumpolar herbivore known for occupying a unique dietary niche, where they subsist on low-
50 quality vegetation that sympatric herbivores tend to avoid (Festa-Bianchet et al. 2011; Mallory
51 and Boyce 2018). Here, we present a systematic review of the biogeographic, temporal, and
52 biological predictors of intra-specific dietary variation for caribou, a globally threatened species
53 with a circumpolar range.

Across their biogeography, caribou are predominantly thought to be specialist lichen consumers, especially during the winter (Bergerud 1974; Thomas and Hervieux 1986; Heggberget et al. 2002). Similar to other ungulates living at high latitudes, caribou are physiologically adapted to survive on reduced quality and quantity of food when resources are scarce (White 1983; Heggberget et al. 2002). Caribou are thought to specialize on lichens because they are abundant throughout Boreal and Arctic ecosystems and they are readily digested and high in digestible energy (Thomas and Hervieux 1986; Barboza et al. 2020). However, despite the benefits to lichen specialization, lichens contain less protein than required for maintenance by most Boreal and Arctic ungulates (Parker et al. 2005). Further, caribou diet can be, and often is, more generalized (Bergerud 1972; Schaefer et al. 2016; Denryter et al. 2017; Zhao et al. 2019). As highlighted by Denryter et al (2017), limited year-round data and the difficulty of obtaining data in the winter may be responsible for the assumption of lichen specialization. Caribou diet varies throughout their range, presumably as a function of variation in availability of different forage species and variation in direct and indirect competition from sympatric ungulates (Heggberget et al. 2002; Mallory and Boyce 2018).

Competition for caribou is often predator mediated (Seip 1992). Apparent competition occurs when two prey species share a predator and can affect the distribution and abundance of either prey species (Holt 1977). For instance, apparent competitive exclusion between caribou and sympatric ungulates may influence caribou diet. For caribou, apparent competition tends to occur when sympatric ungulates, e.g., moose (*Alces alces* (Linnaeus, 1758)) and white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)), undergo northern range expansion (Latham et al. 2011b; Serrouya et al. 2017). As a result, predators such as wolves (*Canis lupus* (Linnaeus 1758)), whose primary prey are other ungulates, have a negative effect on caribou, which are

typically more vulnerable prey than moose (Serrouya et al. 2021). Although the effect of apparent competition among sympatric ungulates on diet remains unknown, it may affect caribou foraging behaviour (Klein 1991; Mallory and Boyce 2018).

Foraging theory predicts that competition can increase dietary specialisation as a result of competitive exclusion (Hirzel and Le Lay 2008), while temporal variability in habitat quality may favour dietary generalists (Wilson and Yoshimura 1994). Caribou live at the intersection of these dichotomies, often co-existing with several sympatric ungulate competitors while also occupying highly seasonal ecosystems. Thus, temporal and biogeographic variation in forage availability and competition could influence caribou diet. In the arctic, for example, Peary caribou (*Rangifer tarandus pearyi* (Allen 1902)) and muskoxen (*Ovibus moschatus* (Zimmerman 1780)) spatially overlap and may compete for resources and space (Jung et al. 2015; Jenkins et al. 2020). By contrast, in another part of their biogeography, the boreal forest, caribou and moose consume different forage species (Christopherson et al. 2019) and select different habitats (James et al. 2004; Dickie et al. 2020). Although caribou have different nutritional and spatial requirements than most of their sympatric competitors, in the absence of competitors they may expand their dietary, and thus spatial, niches.

Given the importance of nutrition to reproductive success for caribou (Crête and Huot 1993; Denryter et al. 2020), accurately characterising caribou diet throughout their range is essential to ensure appropriate forage is available. Moreover, a generalized species-wide, i.e., biogeographic, determination that caribou are lichen specialists may be overly simplified and has potential to misinform management decisions that fail to protect locally important foraging areas. We conducted a systematic review of published studies quantifying diet for *Rangifer* across its biogeographic range. Based on a series of conservative inclusion criteria (see Materials and

Methods), we identified 30 studies that present data on the proportion of a given plant type in caribou diet (for list of studies and references see Table S1). Using data presented in these studies, we investigated the effects of temporal (i.e., season), biogeographic (i.e., caribou ecotype and net primary productivity), and biological (i.e., inter-specific competition measured as the number of sympatric ungulates in the study area) variables on the proportion of lichen, graminoids, and non-graminoid vascular plants (hereafter, vascular plants) observed in caribou diet. Using these data, we tested three hypotheses.

H1) We hypothesized that caribou diet would be influenced by temporal variation (i.e., season) in environmental factors that influence the availability of different plant groups. We predicted that lichen would represent a higher proportion of diet in winter compared to other seasons due to the year-round availability of lichen in northern ecosystems.

Meanwhile, although lichen remains available during warmer seasons, such as calving and summer, we predicted caribou diet in warmer seasons would be composed primarily of more nutritious food, such as graminoids and other vascular plants (e.g., forbs and shrubs).

H2) We hypothesized that caribou diet would be influenced by biogeographic variation, (i.e., measured as ecotype and net primary productivity), in environmental factors that influence the availability of different plant groups. Given that caribou and reindeer have a circumpolar range, we tested if spatial variation in diet may represent two non-mutually exclusive factors: net primary productivity and ecotype. Climatic differences between regions determines the community of available vegetation and we predicted that caribou living in less productive environments would consume a higher proportion of lichen.

Second, we predicted that differences in behaviour and ecology between geographically

distinct *Rangifer* ecotypes would result in dietary differences. Given the lack of research comparing diet for caribou ecotypes (but see Heggberget et al. 2002), we had no *a priori* prediction about how ecotypes might differ from one another.

H3) We hypothesized that variation in direct and indirect competition (i.e., species richness of sympatric ungulates) would influence caribou diet. Caribou are often characterised as selecting low-productivity habitat types and marginal forage species, in contrast to other ungulates that select for high-productivity early successional forests and more nutritious forage. Specifically, through competition or apparent competition caribou may be excluded from accessing more productive and thus more nutritious forage. Even though caribou and their competitors may not be competing for the same forage species, we predicted that in systems where caribou co-occur with a greater number of sympatric ungulates, the proportion of lichen in their diet would be higher than the proportion of vascular plants. By contrast, we predict that in systems where caribou co-occur with fewer sympatric ungulates, the proportion of vascular plants in caribou diet would be higher than lichen.

H1 and H2 concern the temporal and biogeographic spatial variation in the availability of plants at a given time or in a given place. Conversely, H3 concerns whether caribou can access the plants that are available when access is limited by competition and apparent competition.

Materials and Methods

Literature search

To evaluate biogeographic variation in *Rangifer* (hereafter, caribou) diet in the peer-reviewed literature, we conducted a literature survey using Thomson's Scientific Web of Science core databases. We conducted our literature survey up to and including papers published in 2020 using a range of search terms that were likely to yield articles on caribou diet. Our searches were conducted between January and March 2019 and an updated search in May 2020. We conducted systematic searches of keywords on Web of Science that generated lists of articles that were likely relevant for our analysis. We searched 'caribou' or 'reindeer' in combination with either 'forag*' or 'diet' coded as either the title or topic in the search. Based on each combination of terms, we filtered articles by determining whether they collected or presented data on caribou diet. After identifying selected articles from our Web of Science search, we cross-referenced our list with the studies reviewed by Heggberget et al. (2002). Of the 15 articles presented in Table 1 from Heggberget et al. (2002), 6 were captured in our original Web of Science search and we added the additional 9 studies to our analysis. Finally, given that the journal '*Rangifer*' has been inconsistently indexed through time and several key papers that were missed in our Web of Science searches were published in *Rangifer*, we systematically searched through the table of contents for the journal *Rangifer* between 2002 (i.e., the year Heggberget et al. 2002 was published) and 2020. We did not search table of contents prior to 2002 because we assumed all relevant articles published prior to 2002 were identified by Heggberget et al. (2002).

In total, we identified 69 articles where data on caribou diet were presented. These included studies that collected dietary data based on microhistological, cuticular, or DNA analysis of fecal samples ($n = 25$ articles), rumen contents ($n = 16$ articles), visual observation of

caribou eating in the field ($n = 9$ articles), visual signs that caribou had foraged on plants in the field ($n = 7$ articles), visual observation of caribou foraging from video cameras affixed to collars ($n = 5$ articles), data presented were originally presented in another study ($n = 2$ articles), analysis of pollen and spores in feces ($n = 1$ article), consideration of only a single plant without presenting measurements from other plant species or groups ($n = 1$), or directed sampling of plants ($n = 1$ article). We were unable to access two articles and a third article had no description of the methods. To ensure data on diet composition were comparable across studies, we restricted our analysis to only include articles that presented proportion of diet composition using fecal samples or rumen contents ($n = 30$). We selected these two methods of data collection because they present an opportunity to quantify the proportion of a given plant type in the diet and to compare differences in the composition of caribou diet across studies through space and time. By contrast, studies that identified diet using DNA or visual observation are typically unable to quantify an absolute proportion of a given plant species consumed (Garnick et al. 2018). For the 30 articles that met our criteria, we extracted information on the proportion of diet attributed to several variables of interest (see below). For a single study (Mathiesen et al. 1999), we excluded data for reindeer on South Georgia Island as this population is an outlier in terms of both latitude and forage availability, but we retained the dietary data presented in this study for Reindeer in Norway. We acknowledge that other factors influence the use of resources, for example, selection as a function of availability (Northrup et al. 2021). We did not, however, attempt to control for the availability of specific forage at each study location, as that information was unavailable within the papers in our analysis. We were also unable to include information on demographic (i.e., age or sex) variation in diet because most studies did not present information on sex- or age-specific diet.

Data extraction

Taxonomic variation of plants: For each study, we extracted the average proportion of different plant species or taxonomic groups consumed by caribou. In cases where diet data were presented at the species level, we grouped plant species into one of nine broad taxonomic groups (lichen, graminoids, shrubs, forbs, horsetails, trees, moss, fungi, and other plants). Plants in the ‘other’ category included liverworts, seaweed, rhizomes, and rushes. We did not consider instances where caribou were found to consume animal parts and litter. In most cases, dietary data were presented as averages in text or tables and were often broken down into temporal (e.g., season or year) or spatial (e.g., study sites or populations) categories. For eight articles, data were not available in text or tables, but were available in figures, from which we extracted data using the digitize package in R (Poisot 2011). For subsequent analyses predicting the proportion of a given plant type in caribou diet, we grouped plants into three broad categories: vascular plants (including shrubs, forbs, and trees), graminoids (grasses and sedges), and lichen. Other plant categories (i.e., horsetails, moss, fungi, and other plants) comprised a relatively small proportion of the overall diet and were excluded from further statistical analyses.

Temporal variation: For each study, we determined in which season data were collected based on existing categories used by the authors or, if categories were not defined but sampling dates were provided, we assigned data to one of five biologically relevant seasons for caribou (Bastille et al. 2013; Bastille-Rousseau et al. 2016): calving (June), summer (July and August), autumn (September–November), winter (December–March), and spring (April and May). In cases where an article presented averages for different years (or groups of years) or locations, we considered each year (or group of years) or location as an independent data point in subsequent analyses.

210 Thus, the number of data points retained for subsequent analysis varied for each article (total =
211 156, mean = 5 data points per article, range = 1–18 data points per article).

212 *Spatial and climatic variation:* We calculated net primary productivity associated with the
213 general area of each study using Google Earth Engine (Gorelick et al. 2017). Specifically, we
214 extracted the approximate centroid of the herds included in each article either based on
215 coordinates presented in the article or based on the approximate location of the herd studied in
216 the article. We then sampled average annual net primary productivity (Running and Zhao 2019)
217 within a 50 km circular buffer around each set of coordinates. Given the range of years that data
218 were collected in our study (i.e., 1950s to 2010s), and the lack of available productivity data
219 prior to 2000, we standardized net primary productivity by calculating the average annual net
220 primary productivity for each herd over a 20-year period (2001–2020). While this approach does
221 not provide a measure of temporal variability in net primary productivity, it does provide spatial
222 variability experienced by each herd. We also separated caribou into subspecies or ecotypes
223 (hereafter, ecotype) based on either assignment by the authors or the region in which the study
224 took place. Ecotypes included Peary caribou *Rangifer tarandus pearyi*, barren-ground caribou
225 (*R.t. groenlandicus* (Borowski 1790), including Greenland caribou, mountain (*R.t. caribou*),
226 woodland (*R.t. caribou*), reindeer *R.t. fennicus* (Lönnerberg 1909), and introduced reindeer (*R.t.*
227 *fennicus*).

228 *Interspecific competition (direct and/or indirect):* To assess interspecific competition, we
229 determined the number of sympatric ungulates in the same geographic area as the herd studied in
230 each article. Specifically, we visually examined range maps of ungulates and identified eleven
231 different sympatric ungulate species throughout the range of caribou and reindeer. Sympatric
232 ungulates included: moose (*Alces alces*), bison, (*Bison bison* (Linnaeus, 1758)), elk (*Cervus*

canadensis (Erxleben 1788)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), white-tailed deer (*O. virginianus*), mountain goat (*Oreamnos americanus* (Blainville, 1816)), muskox (*Ovibos moschatus*), bighorn sheep (*Ovis canadensis* (Shaw, 1804)), Dall sheep (*O. dalli* (Nelson, 1884)), roe deer (*Capreolus capreolus* (Linnaeus 1758)) and red deer (*C. elaphus* (Linnaeus 1758)). In total, the range of sympatric ungulates for a given study was 0–6. In cases where captive caribou or reindeer were studied, we considered these herds to have 0 sympatric competitors. Meanwhile, due to the relatively small number of studies with 5 ($n = 1$ study) or 6 ($n = 1$ study) sympatric ungulates, we used pooled data for studies with ≥ 4 sympatric ungulate species for subsequent analyses.

Statistical analysis

Our first objective was to determine the species of plants consumed by caribou and the frequency these plants were recorded in different studies across their range. Given the unrealistic expectation of equal representation of plant groups (i.e., the assumption required for a chi-squared test to assess differences in proportions of plant groups) and the difficulty in estimating availability of plants at such a broad scale, we present summary data as the proportion of plant groups identified in each study. Our second objective was to determine the collective effects of four ecological variables on caribou diet: season, caribou ecotype, latitude, and sympatry with other ungulates. We generated three model sets to examine the effect of fixed effect variables on the proportion of each plant type (i.e., lichen, graminoids, and vascular plants) observed in the diet of caribou from a given study. Thus, our unit of analysis was not always at the level of a single study, but rather, it was the proportion of each plant type presented based on spatial or temporal breakdown provided in each study. We used linear mixed effects models from the glmmTMB (Brooks et al. 2017) package to account for potential variance among studies. In

addition, glmmTMB models are equipped to deal with proportional data as the response variable and we fit each model with the beta distribution for proportional data (Douma and Weedon 2019). We used Akaike Information Criteria for small sample sizes (AICc) and our global models included net primary productivity, season (calving, summer, autumn, winter, or spring), caribou ecotype (Peary, barren-ground, mountain, woodland, reindeer, or introduced reindeer), the number of sympatric ungulate species within the range of a caribou herd, and the data collection method from the study (rumen or fecal) as fixed effects. We then iteratively removed covariates, and combinations of covariates, and used AICc model selection to assess the most parsimonious model for each plant group (Table S2). We retained data type in all models to account for this variable in coefficient estimates of more biologically relevant covariates. All models included study ID as a random effect.

Results

Plants

Based on the 30 articles that met the criteria for our study, 17 provided data on plant species, while the other 14 broadly classified plants into groups. In the 17 articles that provided data on plant species, we identified 409 occurrences of plants consumed by caribou, including 130 unique species from 85 genera (Table 1). Based on the assignment of all plants to broad taxonomic groups, lichens accounted for 21.0% (86/409 occurrences), graminoids accounted for 15.6% (64/409 occurrences), shrubs accounted for 17.6% (72/409 occurrences), and forbs accounted for 17.1% (70/409 occurrences) of plants consumed by caribou (Table 1).

The most common genera were *Salix* (at least 1 of 5 *Salix* species identified in 9/17 articles that provided data on plant species), *Equisetum* (at least 1 of 2 *Equisetum* species identified in 7/17 articles), *Dryas* (at least 1 of 3 *Dryas* species identified in 7/17 articles), *Cladonia* (at least 1 of 4 *Cladonia* species identified in 5/17 articles), and *Vaccinium* (at least 1 of 5 *Vaccinium* species identified in 7/17 articles).

Lichen model

The top model included season, ecotype, primary productivity, and data type (marginal $R^2 = 0.74$; Table 2), although the number of sympatric ungulates also appeared in models that were $< 3 \Delta AICc$ from the top model (Table S2). We found the proportion of lichen in caribou diet varied seasonally, such that the proportion of lichen in caribou diet was lowest in calving and summer, but increased in autumn, winter, and spring (Table 2; Figure 1). We also found that among ecotypes, barren-ground and mountain caribou had the highest proportion of lichen in their diet, while Peary caribou and reindeer had the lowest proportion of lichen in their diet (Table 2; Figure 2). There was a positive, but non-significant, relationship between primary productivity

and the proportion of lichen in caribou diet (Table 2; Figure 4). There was no effect of data type on the proportion of lichen in caribou diet (Table 2).

Graminoid model

The top model included primary productivity and the number of sympatric ungulates and data type (marginal $R^2 = 0.68$; Table 2), although models including season appeared in models $< 3 \Delta AICc$ of the top model (Table S2). The effect of the number of sympatric ungulate species was negative (Table 2), suggesting that as the number of sympatric ungulates increased, the proportion of graminoids in caribou diet decreased (Figure 3). In contrast to the effect for lichen, there was a negative relationship between primary productivity and the proportion of graminoids in caribou diet (Table 2; Figure 4). Although season was not included in the top model, we found the proportion of graminoids in caribou diet was lowest in winter and spring compared to calving, summer, and autumn (Figure 1). Similarly, although ecotype was not included in the top model, we found contrasting patterns to those we observed for lichen. Specifically, Peary caribou and reindeer had the highest proportion of graminoids in their diet, while barren-ground and mountain caribou had the lowest proportion of graminoids in their diet (Figure 2). Studies that collected dietary data from rumen samples had higher representation of graminoids in the diet compared to studies that collected dietary data from fecal samples (Table 2).

Vascular plants model

The top vascular plants model included season, primary productivity, and data type (marginal $R^2 = 0.23$; Table 2), although the number of sympatric ungulates appeared in models $< 3 \Delta AICc$ of the top model (Table S2). We found the proportion of vascular plants in caribou diet was lowest in winter, autumn, and spring compared to calving and summer (Table 2; Figure 1). The effect of primary productivity on the proportion of graminoids in caribou diet was slightly negative,

314 although this relationship was not significant (Table 2). Although it was not in the top model, the
315 effect of the number of sympatric ungulate species on the proportion of vascular plants
316 consumed was negative, but not significant (Table 2), suggesting that as the number of sympatric
317 ungulates increased, the proportion of vascular plants in caribou diet also decreased (Figure 3).
318 There was no effect of data type on the proportion of vascular plants in caribou diet (Table 2).
319 For visualization of effect sizes from all top models, i.e., model coefficients, see Figure S1.

Draft

Discussion

For decades *Rangifer* diet has been widely described for individual populations and our systematic review unifies the descriptive nature of these studies to test biologically relevant hypotheses about dietary variation through time and biogeographic space and as a function of competition. For species typically considered specialized foragers, dietary niche width can be highly variable and, in some cases, dietary generalization occurs. We found caribou and reindeer consume at least 130 different plant species across their biogeographic range. Indeed, caribou and reindeer are commonly considered lichen specialists, but our systematic review collated data from published studies and suggests that caribou can, and do, consume a diversity of plants depending on the seasonal and geographic availability of resources.

As expected, caribou diet varied seasonally. Consistent with our hypotheses and common discourse, lichen constituted the largest portion of diet during the winter (Bergerud 1974; Thomas and Hervieux 1986; Gaare 1997; Heggberget et al. 2002; Newmaster et al. 2013; Denryter et al. 2017). During calving and summer, lichen consumption decreased and was replaced primarily by graminoids, but other vascular plants, including shrubs and forbs, also increased in prevalence. Given that newly emergent vascular plants are higher in protein and lower in fibre relative to lichen, seasonal changes in diet based on the availability of emergent vegetation that corresponds with parturition and lactation is an intuitive outcome (Parker et al. 2009; Thompson et al. 2015). During lactation (spring-summer) protein requirements increase for female caribou by 110-130% compared to winter requirements (Barboza and Parker 2008). Corroborating past work studying caribou energetic expectations, we found the proportion of vascular plants consumed during calving and summer seasons was higher than in other seasons. An alternate explanation for consuming more protein rich forage during calving and summer is

that caribou tend to lose weight throughout winter (Tyler et al. 1999) and have a negative protein balance after primarily consuming lichen during winter (Gerhart et al. 1996; Parker et al. 2009). While lichen consumption varies seasonally, graminoid consumption was consistent throughout the year, suggesting that caribou likely supplement lichen consumption with senescent vegetation during winter (Parker et al. 2005). Relative to lichen, graminoid consumption was relatively low (~10-20% of seasonal diets composed of graminoids) presumably because graminoids are less digestible compared to other vascular plants (Barboza et al. 2018). Our results affirm known ecology in caribou (e.g. Parker et al. 2009; Barboza et al. 2018; Denryter et al. 2020), which suggests a relatively consistent seasonal pattern of diet: caribou primarily consume lichen in winter and vascular plants in summer.

Despite physiological and energetic trade-offs that govern differences between summer and winter diet for caribou, the effect of predators on caribou space use and diet requires consideration. Wolves and black bears (*Ursus americanus* (Pallas 1780)), are the primary predators for caribou throughout most of their range in North America, e.g. Quebec (Leblond et al. 2016), Ontario (Fryxell et al. 2020), and Alberta (Dickie et al. 2020). In most cases, caribou separate themselves from other ungulates and consequently also wolves and black bears by selecting mature boreal forests and less productive wetlands (Bowman et al. 2010). However, early seral stage forests with hardwood and mixed wood stands are favourable for sympatric ungulates, i.e., moose and white-tailed deer, and thus these habitats tend to have higher predator abundances (Neufeld et al. 2021). Mature boreal forests tend to have productive lichen communities (Greuel et al. 2021), while early seral stage forests tend to have higher primary productivity and higher vascular plant and graminoid abundance. Caribou therefore trade-off access to productive forage and predation. We found caribou consumed higher proportions of

lichen in winter; a result corroborated by analyses of caribou habitat selection (Fortin et al. 2008; Joly et al. 2010; McGreer et al. 2015) suggesting that caribou tend to select mature forests with high lichen abundance in winter (Mallory and Boyce 2018). Conversely, similar decisions in summer and calving are more nuanced. For example, we found that caribou consumed higher proportions of graminoids and vascular plants in calving and summer. Plant types that are presumably more abundant in productive ecosystems with a higher diversity of sympatric ungulates and their predators. Thus, despite the increase in apparent competitors and predators in more productive ecosystems, caribou appear to trade-off these risks for the benefits of supplementing a lichen diet with vascular plants. Caribou may select for higher primary productivity, i.e., areas where graminoids or forbs are abundant, in summer if there are no wolves or other competitors (Bergerud et al. 2007). While caribou trade-off access to productive forage to space away from predators and competitors in many areas of their range, counterexamples exist. For example, more productive habitats regenerate more quickly after disturbance, accelerating the return of closed-canopy conifer forests and reducing the window of high predation risk for caribou (Fortin et al. 2017).

We found mixed support for our hypothesis that diet would vary spatially throughout the biogeographic range of caribou based on ecotype and primary productivity. There was a significant negative effect of primary productivity on the proportion of graminoids consumed by caribou and a positive trend suggesting the proportion of lichens consumed by caribou increases with primary productivity. We cautiously interpret a positive relationship between primary productivity and lichen consumption, as it opposes previous findings for caribou (e.g. Denryter et al. 2017). A positive effect of productivity on lichen consumption likely highlights the trade-off between predation and foraging: as ecosystems become more productive and therefore support

higher densities of competitors and shared predators, caribou are more likely to space away from productive habitats at smaller spatial scales and thus consume lichen. By contrast, in less productive environments, that support a lower density of competitors and thus fewer shared predators, caribou are more likely to be free to consume graminoids. As noted by Rettie and Messier (2000), caribou avoid predators, but predator-free habitats must still provide resources with which caribou can meet their dietary needs.

Diet varied by caribou ecotype. We found that woodland, mountain, and barren-ground caribou had relatively high proportions of lichen in their diet. However, Peary caribou and reindeer relied less on lichen and had the highest proportion of graminoids in their diet. The likely explanation for these differences between ecotypes is availability of lichens compared to other plants. Although we were unable to incorporate estimates of availability in our models, we assumed that lichens are present in Boreal and Tundra ecosystems, but High Arctic islands, like those inhabited by Peary caribou and some reindeer, e.g. Svalbard, support relatively low lichen biomass and caribou tend to consume willow and graminoids (Klein 1992; Larter and Nagy 1997). Greater consumption of graminoids compared to lichens for more northern ecotypes could also be attributed to High Arctic island populations of Peary caribou (Thomas and Edmonds 1983) and reindeer on Svalbard (Loe et al. 2021) existing at relatively low densities relative to other High Arctic herds (Joly et al. 2009). Survival without lichen in winter appears to be restricted to specific circumstances related to the ecotype and range characteristics of the population in question (Joly et al. 2009; Mallory and Boyce 2018). For example, in the absence of predators caribou often reduce their lichen consumption (Klein 1991), while high-fiber pellets supplement caribou diet in maternal pens (Adams et al. 2019; Heard and Zimmerman 2021). These examples highlight that, regardless of ecotype, caribou that live in circumstances where

predator and competitor density are low (or absent) will predictably reduce their lichen consumption in favour of more nutritious vascular plants.

To standardize our data, our analysis focused only on studies that collected data based on fecal pellets or rumen contents because these methods allow for precise estimation of percentages. However, we suggest that a mixed approach is necessary to continue to disentangle drivers of variation in caribou diet. Historically common techniques, including microhistology, allow for estimation of the proportion of a given plant species or taxa in caribou diet (e.g. Bergerud 1972), however, these techniques may result in low accuracy and taxonomic resolution (Carrière 2002; Newmaster et al. 2013). Novel technological tools such as DNA metabarcoding and video recorders attached to collars (e.g. Newmaster et al. 2013; Christopherson et al. 2019) provide higher resolution insight into the diversity of caribou diet yet are currently limited in their ability to determine the proportion of a given species or plant type (Deagle et al. 2013; Garnick et al. 2018). While some work suggests that there is a high correlation between quantifying diet from cameras and DNA metabarcoding (Newmaster et al. 2013), quantifying diet using DNA metabarcoding should be done cautiously (Garnick et al. 2018). As diet studies shift away from microhistological analysis and towards incorporating more DNA barcoding techniques (Garnick et al. 2018), caribou foraging studies should be careful to use the tools that best fit the research questions at hand. Several works have compared the cost, resolution, timescale, and accuracy of these methods (Newmaster et al. 2013; Garnick et al. 2018) and we suggest that, when possible, future studies should combine traditional and novel methods to best assess the quantity and proportion of specific resources used.

Given that many caribou population are likely limited by predators (Latham et al. 2011a; Serrouya et al. 2021), we assumed the number of sympatric ungulates reflects apparent

competition and not competitive exclusion. We observed trends suggesting the number of sympatric ungulates within the range of a caribou herd had a marginal effect on caribou diet composition. With increasing numbers of sympatric ungulates, caribou consumed greater proportions of lichen, while graminoids and vascular plants constituted a greater proportion of the diet when there were fewer sympatric ungulates. We cautiously interpret these trends to suggest that when apparent competition limits access to food sources. In the presence of competitors, caribou partition their dietary niches and forage primarily on lichen. While we were unable to quantify spatial or dietary niche partitioning among caribou and their sympatric competitors, existing work suggests that caribou partition their space use (Christopherson et al. 2019; Jenkins et al. 2020) and diet (Fischer and Gates 2005; Jung et al. 2015) in the presence of competitors. When apparent competition is reduced and density of sympatric ungulates and predators is low, caribou appear to increase consumption of graminoids relative to lichens. Such results have consequences for land management as sympatric species such as moose and white tailed deer experience range expansions (Klein 1991; Mallory and Boyce 2018).

Caribou populations are in decline throughout their range (Festa-Bianchet et al. 2011; Mallory and Boyce 2018). Most declines have been attributed to disturbance and climate change (Sharma et al. 2009; Festa-Bianchet et al. 2011; Bernes et al. 2015; Table 3). In the caribou diet zeitgeist lichen has played an outsize role, but our biogeographic analysis of caribou diet has three central themes highlighting the importance of a varied diet for caribou. First, caribou diet varies seasonally with lichen consumption highest in winter and vascular plant consumption highest during calving and summer; 2) caribou consume more nutritious food (i.e., vascular plants) when they can; 3) the opportunity to consume vascular plants is likely mediated by availability of these plants in combination with apparent competition. Conservation practices

458 often focus on the protection of habitat to ensure population persistence, and so identifying the
459 most valuable habitat characteristics for caribou populations is key (Nagy-Reis et al. 2021).
460 Considering variation in caribou diet may contribute some nuance when making decisions about
461 caribou conservation and our study provides a broad view of caribou diet through their
462 biogeographic range.

Draft

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717 **Table 1:** Summary of nine broad plant groups identified in 30 studies of caribou (*Rangifer*
 718 *tarandus*) diet. Note, some genera occurred in multiple taxonomic groups (e.g., some species of
 719 *Salix* are considered trees and others are considered shrubs).

Taxonomic group	Proportion of occurrence	Frequency of occurrence (of 409 total)	Number of genera
Lichens	21.0%	86	13
Graminoids	15.6%	64	16
Shrubs	17.6%	72	15
Forbs	17.1%	70	25
Moss	13.2%	54	9
Horsetail	3.9%	16	3
Trees	4.1%	17	8
Fungi	0.01%	4	N/A
Other	6.3%	26	5

720 Note: no genera were identified for fungi, for all instances of fungi occurred in caribou diet the
 721 authors simply identified “fungi” and did not provide taxonomic identification.

722

Table 2: summary of the top models from three model sets testing the effects of candidate variables on the proportion of lichen, graminoids, and vascular plants in caribou (*Rangifer tarandus*) diet. Note, model selection results are presented in Table S2 and coefficients can be visually inspect in Figure S1.

Variable	Lichen model			Graminoid model			Vascular plants model		
	Estimate ± SE	z-value	p-value	Estimate ± SE	z-value	p-value	Estimate ± SE	z-value	p-value
Intercept	−3.14 ± 0.66	−4.73	<0.001	−1.77 ± 0.20	−8.86	<0.001	−0.46 ± 0.31	−1.48	0.14
Ecotype									
-Barren-ground	2.29 ± 0.68	3.34	<0.001	—	—	—	—	—	—
-Mountain	3.41 ± 0.87	3.91	<0.001	—	—	—	—	—	—
-Woodland	2.08 ± 0.81	2.58	0.01	—	—	—	—	—	—
-Reindeer	0.99 ± 0.61	1.63	0.10	—	—	—	—	—	—
-Introduced reindeer	2.48 ± 0.83	3.00	0.003	—	—	—	—	—	—
Season									
-Summer	0.28 ± 0.27	1.06	0.29	—	—	—	−0.13 ± 0.28	−0.46	0.64
-Autumn	1.16 ± 0.27	4.25	<0.001	—	—	—	−0.81 ± 0.29	−2.82	0.004
-Winter	1.23 ± 0.26	4.82	<0.001	—	—	—	−1.02 ± 0.28	−3.72	<0.001
-Spring	0.82 ± 0.27	3.01	0.003	—	—	—	−0.77 ± 0.29	−2.60	0.01
Primary productivity	0.23 ± 0.23	1.00	0.32	−0.23 ± 0.11	−2.06	0.03	−0.008 ± 0.13	−0.06	0.95
Number of sympatric ungulates	—	—	—	−0.14 ± 0.07	−1.88	0.06	—	—	—
Data type (rumen)	−0.50 ± 0.39	−1.29	0.20	1.25 ± 0.24	5.14	<0.001	0.20 ± 0.32	0.61	0.54

Reference category for ecotype variable was Peary caribou and the reference category for season was calving. Marginal R2 for the lichen model = 0.74 and the model was based on 147 observations from 29 studies. Random effects for the lichen model: among study

728 variance = 0.55. Marginal R² for the graminoid model = 0.68 and the model was based on 142 observations from 27 studies. Random
729 effects for the graminoid model: among study variance = 0.22. Marginal R² for the vascular plants model = 0.23 and the model was
730 based on 147 observations from 29 studies. Random effects for the vascular plants model: among study variance = 0.48.

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731 **Table 3:** Four key ecological phenomenon that may affect caribou (*Rangifer tarandus*) diet.

Ecological phenomena	Discussion and influence on caribou diet
Effect of changing plant phenology on caribou diet.	Plant phenology can significantly impact calf survival (Post et al. 2003; Kerby and Post 2013). As a result, changes in the timing of plant emergence in the spring may influence the forage available to female caribou. Caribou typically time parturition to coincide with peak emergence of vegetation (Laforge et al. 2021). Given that caribou appear to consume a relatively large proportion of vascular plants during calving (Figure 1), changes in the emergence of these plants could affect calf survival and ultimately influence population dynamics.
Shrubification	Warming climates have led to the expansion of shrubs into Arctic ecosystems, with possible impacts for climate feedbacks and nutrient cycling (Myers-Smith et al. 2011). Grazing on shrubs by ungulates, such as caribou, may help mitigate the effects of shrubification on the system (Verma et al. 2020). We grouped shrubs with other vascular plants for analyses and although we found no effect of primary productivity, we found that Peary caribou tend to consume higher proportions of vascular plants than lichen (Figure 2), lending support to the hypothesis that caribou could help mitigate shrubification through grazing.
Disturbance mediated apparent competition and direct competition.	Disturbance mediated apparent competition is the human-mediated change in herbivore communities that attracts predators (i.e., wolves (<i>Canis lupus</i> (Linnaeus 1758))), therefore affecting caribou population dynamics. An increase in disturbed habitats can result in higher moose and white-tailed deer densities, which allows predator density to increase. Further, an increase in linear features allows more efficient movement of predators across the landscape, which collectively results in increased predation of caribou (Serrouya et al. 2021). Few studies have addressed the potential effects of disturbance mediated apparent competition on caribou diet. However, our work indicates that in the presence of more sympatric ungulate species, caribou increasingly occupy a narrower dietary niche with less nutritious food. As habitat disturbance, linear features and climate change result in northern range expansion for resource competitors (Klein 1991; Mallory and Boyce 2018), caribou may begin to further rely on less nutritious resources.
Fire	Fire in the boreal forest is a natural phenomenon and caribou evolved with fire (Klein 1982). However, climate change has resulted in larger fires and longer fire seasons. One consequence of large and frequent stand-replacing fires is that lichen will be completely destroyed (Morneau and Payette 1989; Silva et al. 2019) and lichen may take decades to recover (Klein 1982). Our study highlights the diet of woodland caribou, which live primarily in the boreal forest, is composed largely of lichen (Figure 2), suggesting that fire could compromise caribou diet and habitat use. However, caribou appear relatively resilient to fire, presumably due to their evolved history with this natural disturbance (Dalerum et al. 2007; Silva et al. 2020).

732

Figure captions:

Figure 1: Percent of A) lichen, B) graminoids, and C) vascular plants in caribou diet across five biological relevant seasons extracted from 30 published studies of caribou (*Rangifer tarandus*) diet.

Figure 2: Percent of A) lichen, B) graminoids, and C) vascular plants in caribou diet across six ecotypes extracted from 30 published studies of caribou (*Rangifer tarandus*) diet.

Figure 3: Percent of A) lichen, B) graminoids, and C) vascular plants in caribou diet as a function of the number of sympatric ungulate species extracted from 30 published studies of caribou (*Rangifer tarandus*) diet. The trend line for graminoids (panel B) was predicted based on top models presented in Table 2, but note, we did not include trend lines for lichens (panel A) or vascular plants (panel C) because the number of sympatric ungulates was not present in the top model for these model sets.

Figure 4: Relationship between average annual net primary productivity (kg C/m²) and the percentage of graminoids and lichen in caribou diet extracted from 30 published studies of caribou (*Rangifer tarandus*) diet. Trend lines were predicted based on top models presented in Table 2.

Percent lichens in diet

Percent graminoids in diet

Percent vascular plants in diet

Percent lichen in diet

Percent graminoid in diet

Percent vascular plants in diet

Percentage of plant type in diet

● Graminoid
▲ Lichen