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RESEARCH ARTICLE

A taste of space: Remote animal observations and discrete-choice models provide new insights into foraging and density dynamics for a large subarctic herbivore

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Abstract

1. Competition for resources and space can drive forage selection of large herbivores from the bite through the landscape scale. Animal behaviour and foraging patterns are also influenced by abiotic and biotic factors.
2. Fine-scale mechanisms of density-dependent foraging at the bite scale are likely consistent with density-dependent behavioural patterns observed at broader scales, but few studies have directly tested this assertion.
3. Here, we tested if space use intensity, a proxy of spatiotemporal density, affects foraging mechanisms at fine spatial scales similarly to density-dependent effects observed at broader scales in caribou. We specifically assessed how behavioural choices are affected by space use intensity and environmental processes using behavioural state and forage selection data from caribou (*Rangifer tarandus granti*) observed from GPS video-camera collars using a multivariate discrete-choice modelling framework.
4. We found that the probability of eating shrubs increased with increasing caribou space use intensity and cover of *Salix* spp. shrubs, whereas the probability of eating lichen decreased. Insects also affected fine-scale foraging behaviour by reducing the overall probability of eating. Strong eastward winds mitigated negative effects of insects and resulted in higher probabilities of eating lichen. At last, caribou exhibited foraging functional responses wherein their probability of selecting each food type increased as the availability (% cover) of that food increased.
5. Space use intensity signals of fine-scale foraging were consistent with density-dependent responses observed at larger scales and with recent evidence suggesting declining reproductive rates in the same caribou population. Our results

highlight potential risks of overgrazing on sensitive forage species such as lichen. Remote investigation of the functional responses of foraging behaviours provides exciting future applications where spatial models can identify high-quality habitats for conservation.

KEYWORDS
Caribou, climate, competition, density-dependence, functional response, insect harassment, summer diet

1 | INTRODUCTION

Organisms are distributed across space and time through the process of habitat use (Christiansen, 1975; Fretwell & Lucas, 1970; Holt, 1987). Competition for both space and resources drive habitat use from the bite (i.e. fine) through the landscape (i.e. coarse) scale (McLoughlin et al., 2006; Senft et al., 1987). As animal abundance increases, intraspecific competition to obtain food resources can intensify, and fitness can decline in response (Charnov, 1976; Krebs, 1971; Matthiopoulos et al., 2015). Decisions that animals make to acquire resources should thus change, if fitness is to be maximized, in consideration of a suite of ecological interactions including direct competition (Ronconi & Burger, 2011) and predation-sensitive foraging (Sinclair & Arcese, 1995) due to increased energy expenditures and changes in resource quality and availability. Habitat use can thus present an honest signal of regulating populations and eco-evolutionary processes (Brown & Rosenzweig, 1986; Fortin et al., 2008; Morris, 2011).

According to density-dependent habitat theory, non-territorial animals should first use the highest-quality resources to maximize individual fitness across space and, as animal abundance increases, weaken their use of these areas in search of alternatives with reduced competition (Fretwell & Lucas, 1970). Density dependence is particularly important to the ecology of large herbivore populations, which have evolved to maximize fitness in conditions of high intraspecific density with competition for space, habitat, and resources (Bonenfant et al., 2009). For example, female red deer (*Cervus elaphus*) used high-quality *Agrostis/Festuca* grassland habitats, which increased lifetime reproductive success (LRS), but as deer density increased, LRS declined (McLoughlin et al., 2006). For feral horses (*Equus ferus caballus*), as the population approached carrying capacity, use of areas supporting the highest-quality forage weakened, and use of areas supporting lower-quality vegetation increased (van Beest et al., 2014). Thus, understanding how habitat use changes with density can be instrumental to defining habitat quality and understanding how it is affected by both density-dependent and density-independent processes.

Despite its importance, little is known about the mechanisms driving density dependence in large herbivores at fine foraging scales (Kausrud et al., 2006; Senft et al., 1987), especially in wild populations (Senft et al., 1987). Most previous studies were done across large spatial scales (e.g. McLoughlin et al., 2007) or used proxies for forage like landcover classes (e.g. van Beest et al., 2014, 2016). Finer-scale mechanisms of density-dependent foraging at the bite scale (Senft et al., 1987) are likely consistent with patterns observed at broader scales (McLoughlin et al., 2006, 2007), but few studies have directly tested this assertion. Because functional responses of large herbivores suggest diet choices will change in relation to forage availability (Mysterud & Ims, 1998; Spalinger & Hobbs, 1992), it is unclear if foraging processes observed at finer scales will necessarily scale up to those observed at larger scales (Johnson, 1980). By studying patterns of use and changes across scales of local abundance, density dependent processes across space can be assessed.

Accelerating climate-induced changes in resource availability could further alter mechanisms of density dependence and space use. Climate effects are especially important across the Arctic which is undergoing some of the most rapid, terrestrial-system changes observed across the world (Box et al., 2019; IPCC, 2014). The effects of large-scale climate shifts on demography of large herbivores have been well documented by scientific and indigenous knowledge (Bonenfant et al., 2009; Cunsolo et al., 2020; Gagnon et al., 2020; Post & Forchhammer, 2008; Sæther, 1997). At finer scales of foraging, rain-on-snow (ROS) events can cause population collapses of arctic herbivores (Berger et al., 2018; Mallory et al., 2020; Miller & Gunn, 2003). Warming temperatures are changing vegetation structure and function, altering the availability of quality forages for northern ungulates (Rickbeil et al., 2018; Stark et al., 2021). Weather and climate also interact with other biotic factors (e.g. insect harassment, disease; Witter, Johnson, Croft, Gunn, & Gillingham, 2012; Kafle et al., 2020; Koltz & Culler, 2021). Harassment from parasitic insects affects behaviour, movements, and foraging of large herbivores and is expected to intensify across the Arctic under climate change (Ehlers et al., 2021; Johnson et al., 2021; Joly et al., 2020; Koltz & Culler, 2021; Witter, Johnson, Croft, Gunn, & Gillingham, 2012). Understanding effects of weather and climate on fine-scale foraging and behaviour are thus also critical.

Technological advances of animal-borne GPS video camera collars provide researchers new opportunities to remotely observe not only *what* animals are doing but crucially, *where* they are engaging in behaviours across space and time. For wide-ranging and remote species, observing and classifying behaviours from videos can determine activity budgets (Ehlers et al., 2021; Kaczensky et al., 2019; Pagano et al., 2018) and diet selection (Andersen et al., 2020; Calambokidis et al., 2007; Ehlers et al., 2021; Kane & Zamani, 2014; Krause et al., 2015). Further, advancing techniques for mapping continuous vegetation cover (Macander et al., 2022) and climate data (Copernicus Climate Change Service (C3S), 2017, 19/11/2021) enhance our ability to test for the role of density-dependent and -independent factors influencing fine-scale behaviour and food choices. Discrete-choice statistical models can be paired with spatial video data of behavioural state or foraging choices to test the drivers of behavioural choices at a given location (Cooper & Millspaugh, 1999; McCracken et al., 1998; McFadden, 1981). Discrete-choice models account for the decision-making process of the animal when selecting a resource, as resource availability is allowed to vary over time, across space, and among individuals (Cooper & Millspaugh, 2001; McCracken et al., 1998). Discrete-choice models can also explicitly identify foraging functional responses (Cooper & Millspaugh, 1999; Dupke et al., 2021; van Beest et al., 2016). In this framework, animal behaviour can be directly observed from GPS video camera collars.

We tested predictions of density-dependent habitat theory in summer using discrete-choice models for a large herbivore in a subarctic region of Alaska and Canada. Our study population, the Fortymile Caribou Herd (FMCH; *Rangifer tarandus granti*), provided an ideal opportunity to test for effects of space use intensity, a proxy of spatiotemporal density, on female caribou behaviour and foraging choices because of recent population growth from ~56,000 in 2009 to ~84,000 in 2017, which is likely approaching ecological carrying capacity (Boertje et al., 2017; MacNab, 1985). Most existing models of caribou-vegetation dynamics are based on our understanding that caribou have a negative effect on lichen but very few studies have revealed the exact foraging mechanisms (Caughley & Gunn, 1993; Ferguson & Messier, 2000; Payette et al., 2004). Also, the FMCH is unique compared to neighbouring and genetically similar migratory populations, like the Porcupine Caribou Herd (*R. t. granti*), in that they use core areas of their range throughout the year as opposed to having separate seasonal ranges (Orndahl, 2023). If the FMCH is overgrazing critical areas of their range, meaning preferred forage species are depleted due to excessive grazing and ecological carrying capacity is reduced (Mysterud, 2006), recovery of overgrazed lichens (and thus caribou) could take >50 years (Caughley & Gunn, 1993; Collins et al., 2011). Therefore, it remains critical to assess how caribou diets in summer change with space use intensity. We used behavioural state and foraging data observed from GPS video-camera collars (hereafter referred to as 'video collars') worn by adult female caribou to test for mechanisms of density-dependent foraging during summer (Ehlers et al., 2021). Going beyond Ehlers et al. (2021), who evaluated behaviour and diet without spatial information, we specifically investigated how space use intensity was linked to behavioural and foraging choices using multivariate discrete-choice analysis. We combine animal use as observed through videos and associated GPS locations, vegetation cover, and compared use locations across space and time to consider local competition for food.

We tested the hypothesis that density-dependent responses to space use intensity drives behaviour and foraging choices at a fine spatial scale. Density-dependent habitat theory (Rosenzweig & Abramsky, 1985) predicts a decline in the use of high-quality habitats (e.g. lichen-rich and shrub-rich areas) with increasing animal abundance as observed with the FMCH since 2009 (sensu McLoughlin et al., 2006). As weather can also be an important determinant of caribou behaviour (Hagemoen & Reimers, 2002; Joly et al., 2011) we predict the probability of foraging and foraging on high-quality food items will decline as some weather indices (i.e. temperature, wind) or the presence of other biotic drivers (e.g. parasitic insects) change across space and time.

2 | MATERIALS AND METHODS

2.1 | Study area

The summer range of the FMCH spans 105,000 km^2 across Alaska, the United States and the Yukon, Canada (Figure 1). The migratory FMCH increased from ~56,000 in 2009 to ~84,000 in 2017 (L. Frid, 2021; Boertje et al., 2017), followed by a decline estimated ~58,000 in 2020 (L. Frid, 2021). Thus, there are growing concerns over nutritional limitations arising from heavy grazing pressure on preferred food types (Boertje et al., 2012). Additionally, a large-scale wolf control program was undertaken in the study area from 2004 to 2018, reducing predator density and the potential for top-down population and behavioural regulation (Boertje et al., 2017; Schmidt et al., 2017). Because the FMCH summer and winter ranges overlap extensively, grazing impacts on the summer range also affect portions of the herd's winter range. Vegetation types include spruce (*Picea* spp.) forests, deciduous forests, shrubland, and herbaceous tundra (Ehlers et al., 2021). Treeless herbaceous and alpine tundra dominate landscapes >800 m and provide areas for calving, post-calving and summer aggregations (Boertje et al., 2017).

2.2 | Behavioural, foraging, and spatial locations of animals

2.2.1 | Video-camera collars

In the springs of 2018 and 2019, 30 adult female caribou (2018: $n = 15$; 2019: $n = 15$) were captured and fitted with a GPS-Iridium collar integrated with a camera (VERTEX Plus Iridium V 3.0, Vectronic Aerospace GmbH, Germany; see Ehlers et al., 2021). All animal captures were conducted by the Alaska Department of Fish and Game (ADFG) and approved in accordance with ADFG animal welfare standards (IACUC Permit numbers through ADFG: 0002-2018 and 0002-2019). Video collars recorded a 9-s video every 20 min during daylight hours (14–18 h/day) from 10 May to 10 September 2018 and 2019. The internal GPS recorded spatial locations immediately following each 9-s video recording (see Ehlers et al., 2021).

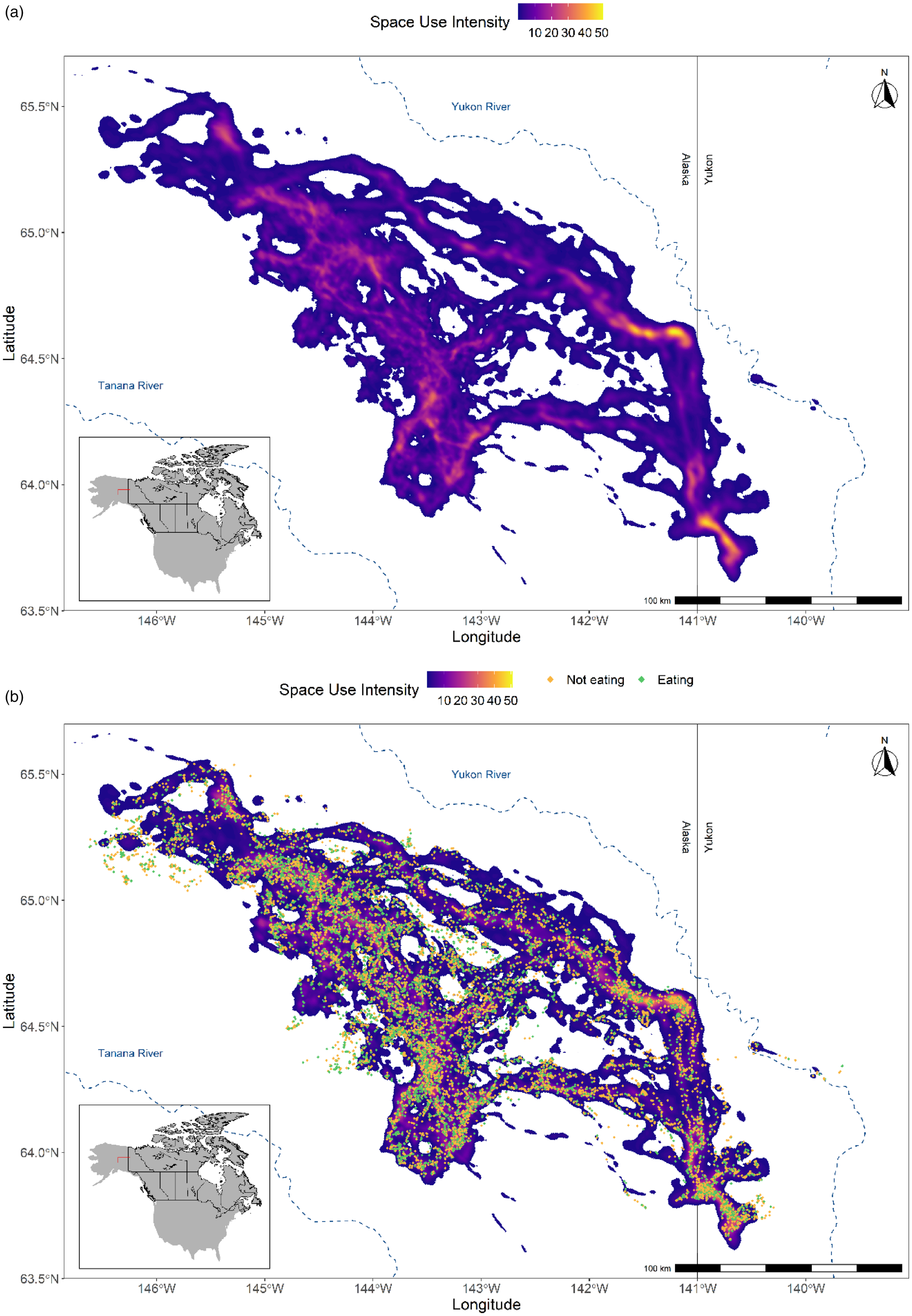
(a)
Space Use Intensity
10 20 30 40 50
Yukon River
Alaska
Yukon
Tanana River
N
100 km
65.5°N
65.0°N
64.5°N
64.0°N
63.5°N
Latitude
146°W
145°W
144°W
143°W
142°W
141°W
140°W
Longitude
(b)
Space Use Intensity
10 20 30 40 50
Not eating
Eating
Yukon River
Alaska
Yukon
Tanana River
N
100 km
65.5°N
65.0°N
64.5°N
64.0°N
63.5°N
Latitude
146°W
145°W
144°W
143°W
142°W
141°W
140°W
Longitude

FIGURE 1 Study area for the Fortymile Caribou Herd (FMCH; *Rangifer tarandus granti*) across Alaska, the United States and Yukon, Canada during summer (May 15–Aug 15) 2018–2019. Relative space use intensities of caribou (a) were estimated as a Brownian Bridge occurrence distribution using annual GPS collar locations for 47 adult females in 2018 ($n=67{,}662$; Table S11). Video camera collar locations ($n=30$ females; b) classifying behaviour as eating (green circles; $n=5549$) or not eating (orange circles; $n=12{,}585$) are overlaid onto the occurrence distribution for visual comparison.

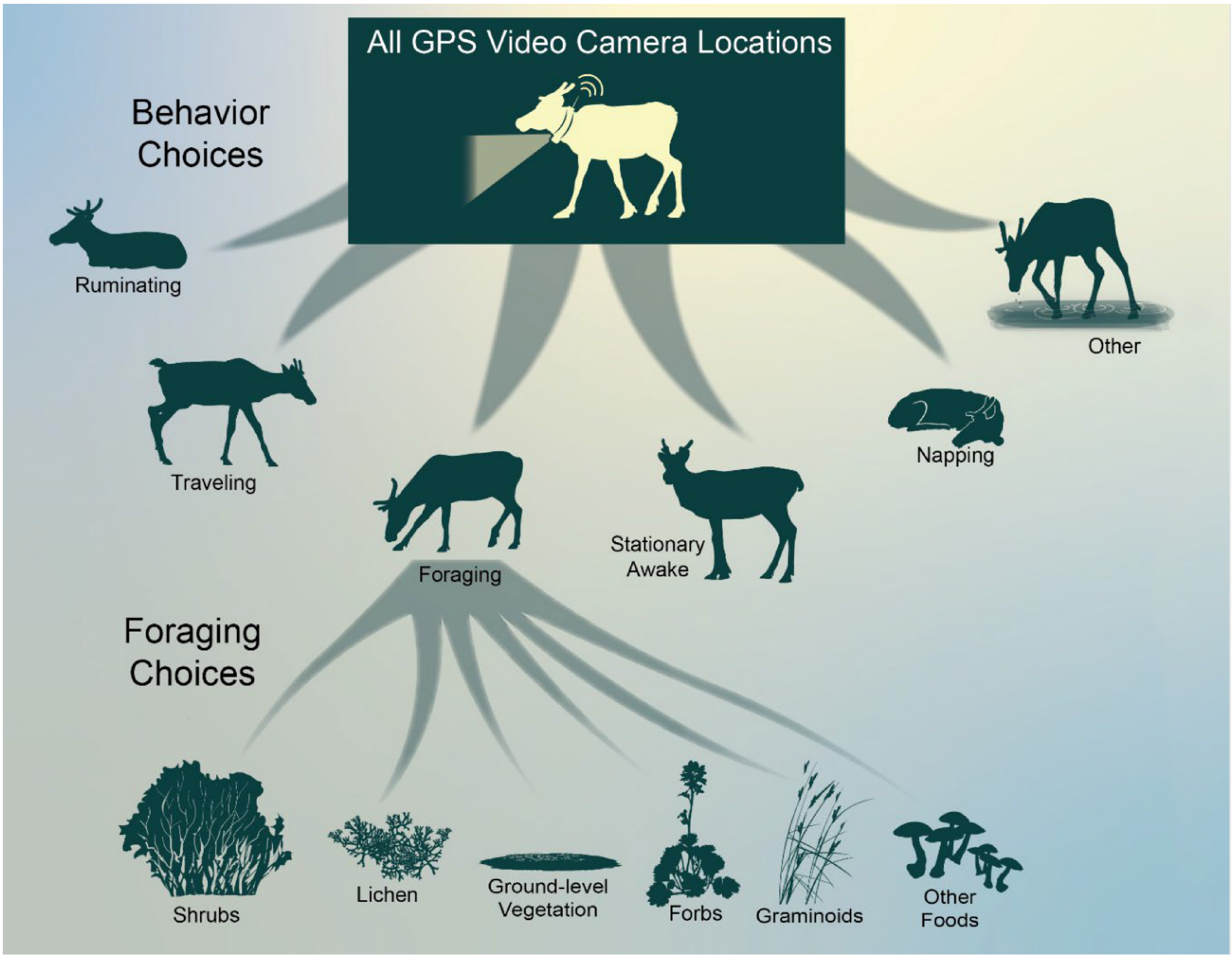

FIGURE 2 Schematic representation of the nested, conditional discrete choices made by female caribou fitted with GPS video-camera collars ($n=30$) across (i) the six observed behaviour categories and (ii) the subsequent conditional discrete choices made among six observed categories of preferred foraging (i.e. food) categories for the Fortymile Caribou Herd, Alaska and Yukon. Conditioned on the caribou being in a particular location (All GPS Video Camera Locations), the dominant behaviour choice was classified and compared to the reference category of rumination. Then, for the subset of foraging choices, we estimated the conditional probability of caribou consuming a particular food group compared to the reference category of ground-level vegetation. Nested probabilities are multiplicative. For example, if the probability of caribou eating (behaviour choice) is 0.5 and the probability of caribou eating lichen (food choice) is 0.5, then the probability of eating lichen is $0.5\times0.5=0.25$.

2.2.2 | Classification of caribou behaviour and foraging from videos

We used video collars to analyse the behaviour and food choices of caribou during summer. We processed data from video collars using a two-phased approach that included both community-science volunteers and botanists (see Ehlers et al., 2021 for details). In 18,134 processed videos, caribou behaviour was classified into six categories for our spatial analysis of behaviour: eating (mean=43.5%), ruminating (25.6%), travelling (14.0%), stationary awake (11.3%), napping (5.1%), or other (0.5%; e.g. drinking, licking soil for minerals, and wading; Figure 2; Ehlers et al., 2021). We removed 44 classified videos that were missing spatial locations due to GPS error, leaving a final sample size of 18,090 behaviour-classified videos for analyses. For our spatial analysis of summer diet, we observed diet in the 5549 videos where caribou were observed eating (behavioural state) and identified 7529 food items (see Ehlers et al., 2021). We then combined food items into six major groups representing the foods we observed caribou consuming: lichen (summer mean = 39.4%), shrubs (36.7%), forbs (6.4%), graminoids (7.0%), ground-level vegetation (8.7%) and other food types (2.6%; includes mushrooms, mosses, *Equisetum* spp. and unknowns; Ehlers et al., 2021).

2.3 | Statistical models

2.3.1 | Discrete-choice model development

Discrete-choice models treat the 'decision maker' (i.e. a caribou), as the sample unit and the selected behaviour or food choice as the observation (Arthur et al., 1996; McCracken et al., 1998). Discrete-choice models can be fit using a variety of approaches, for example, (Hansen et al., 2011) modelled the probability of an animal choosing category A among >2 categories using a conditional multinomial logit regression (McFadden, 1981). However, if all choices are available to, and similar for a caribou, we can estimate the probability of choices using a set of $n-1$ logistic regression models (Cooper & Millspaugh, 1999), where n is the number of categories to be evaluated (e.g. following Dupke et al., 2021). Therefore, we approximated the standard discrete-choice equation using two sets of nested generalized linear models to fit models to caribou choice for (i) behaviours and (ii) food types nested within the foraging behaviour. We then fit a series of conditional binomial logistic regression models where each behaviour or food choice was compared to a common reference category in that choice set (Figure 2). This approach assumed all behaviour and foraging choices were theoretically available to a caribou at each video GPS location. This seems plausible from a behavioural viewpoint; and from a foraging viewpoint, analyses confirmed that most forage species were present even at low cover levels across the study area (see Table S3a).

In our first discrete-choice models (Figure 2), we chose ruminating as the behaviour reference choice as caribou are thought to ruminate relatively indiscriminately across time and space to facilitate digestion (Van Soest, 1982). We refer to this first discrete choice set as the 'behaviour choice' models (Figure 2). We built five independent logistic regression models that included spatial covariates thought to influence behaviour (e.g. Dupke et al., 2021).

Second, for our spatial analysis of summer diet, we chose ground-level vegetation as the reference food choice because it was common across space and time and was a composite of many food items preferred by caribou: lichen, early successional dwarf shrubs, graminoids, forbs, mosses etc. We refer to this second discrete choice set as the 'food choice' models (Figure 2). We built five independent logistic regression models, one for each foraging category excluding the reference category that included spatial covariates thought to influence caribou choice for different foods.

To screen and remove collinear covariates (see Section 2.3.3 and below) in behaviour and food choice models, we fitted univariate generalized linear mixed-effects models using 'lme4' package (R Core Team, 2020) with a binomial (logit) link (Bates et al., 2015). Models were fit to all behaviours and food choices separately. These models included an individual identity random intercept to account for differences in sample sizes between individuals (Gillies et al., 2006). Screening against collinear (or confounded) covariates was done using recommended guidelines of $r \geq |0.6|$ (Menard, 2002; see Figures S3b–S5). For collinear or confounded covariates, we retained the most statistically significant variables (based on p-value). From this reduced set of non-collinear covariates, we started our full multivariate discrete-choice model selection.

2.3.2 | Model selection

We considered the ecological, biotic, and abiotic covariates found to affect caribou behaviour and foraging in the univariate covariate screening for model selection of our final discrete-choice models (Bartoń, 2022). For our multivariate discrete choice models, we conducted model selection using the more conservative Schwarz or Bayesian information criterion (BIC; Brewer et al., 2016) using the R package MuMIn (Bartoń, 2022) and the 'dredge' function to identify the top model using ΔBIC values. We opted for the simpler model for each behaviour and food choice when uninformative covariates were retained (e.g. Arnold's rule; Arnold, 2010). However, because our focus was on testing questions of density dependence and space use, we retained caribou space use intensity, shrub cover, lichen cover, and abiotic drivers of insect presence because of their relevance to our ecological hypotheses regardless of their statistical strength. We selected our top behaviour and food choice logistic regression models using k-folds cross validation across all caribou, and also grouped by individuals (Boyce et al., 2002). We partitioned caribou locations in each discrete-choice dataset D into S subsets. Then, we fit a model to $D-S$ and tested the model against S. We used five folds and 10 bins to generate a Spearman's rank correlation (r_s) for each behaviour- and food-choice model.

2.3.3 | Model covariates

We included a variety of time-varying and static covariates based on previous studies of caribou to assess their influence on caribou behaviour and food choices. We also considered linear and quadratic relationships for covariates and assessed potential non-linearities using generalized additive models (GAM's); but only considered a priori interactions specified below. We used the 'terra' package in R to annotate spatiotemporal data (e.g. weather, windspeed) to spatial locations of caribou (Hijmans et al., 2021).

Relative caribou space use intensity

To test if density dependence influenced behaviour and food choices of caribou, we included covariates representing cumulative caribou space use intensities (estimated over 9 years from 2011 to 2019) and annual space use intensities matching the summer seasons of our study (2018 and 2019). We considered the possibility that temporal scale was important and that the effects of space use intensity were not just based on the current year, but as the result of long-term, cumulative, herbivory since lagged effects have often been reported in large ungulates (Caughley & Gunn, 1993; Forchhammer et al., 2002). The hypothesis is that cumulative long-term space use intensity could affect current behavioural state and food choice, consistent with resource depletion. We estimated both current and cumulative space use intensities using occurrence distributions (ODs) derived from Brownian bridge movement models run in the 'amt' R package (Signer et al., 2019) after resampling telemetry locations at a consistent 5-h relocation interval from other (non-video) GPS collared females in the FMCH between 2011 and 2019 (n = 272; Tables S11 and S12). We considered the effect of population growth on occurrence distributions and weighted each OD for annual population size of the FMCH (L. Frid, 2021) to see if these population-weighted estimates for space use intensity explained additional variation in the data.

Vegetation community cover

We used annual, continuous layers of vegetation cover as covariates in our discrete choice models. These layers estimated top cover of several vegetation communities throughout the FMCH summer range based on a combination of ground and aerial vegetation plot surveys paired with remote sensing data (Macander et al., 2022; Nawrocki et al., 2020). To investigate fine-scale food choices, we included the following vegetation communities in our models: conifer and broadleaf trees, evergreen, and deciduous shrubs (including separate models for each *Alnus* spp., *Betula* spp., and *Salix* spp. shrubs), forbs, graminoids and light-coloured macro-lichens (hereafter, 'lichen'). We expected selection for areas of their range with increased lichen and shrub covers during summer (Ehlers et al., 2021).

Weather and wildfire

We used the meteorological daily aggregate weather data from the Copernicus satellite (Copernicus Climate Change Service (C3S), 2017) and included four daily-averaged parameters: 2-m air temperature, total precipitation, and two components of 10-m wind speeds (eastward and northward). These environmental covariates affected FMCH caribou habitat selection in general at larger scales in Palm et al. (2022), and thus we expected them to potentially affect specific behaviours or foraging here. We matched weather data to the date and location of caribou video recordings. We also included a Landsat based snow persistence (first snow-free date) product at 30-m resolution generated from (Macander et al., 2015) as a spatial covariate in our models. Areas with extended snow persistence are important refugia habitats for insect harassment (Hagemoen & Reimers, 2002) and predict forage quality in the early growing season (Johnson et al., 2021; Skogland, 1980). We expected caribou to select areas with remnant snow in summer to avoid insects (behaviour) but avoid these areas while foraging. Burns have also been shown to strongly reduce the probability of caribou resource selection (Palm et al., 2022), thus, we also included wildfire burn footprint data (polygons) collected from both the Alaska Large Fire Database (FRAMES, 2020) and the Canadian National Fire Database (Canadian Forest Service, 2017) for each study summer.

Insects

We noted the presence of insect avoidance behaviours (e.g. shook head, scratched, sought snow patch, kept muzzle to ground, huddled; Morschel & Klein, 1997; Joly et al., 2020) observed in each video that was used to classify behaviour (Ehlers et al., 2021). Insect presence was included as a binary variable in our models. Because insect presence (e.g. mosquitos) and the effects of harassment to caribou are strongly dependent on wind (Witter, Johnson, Croft, Gunn, & Poirier, 2012), we included an interaction term between insects and wind. We expected more movement behaviour and less eating with insect presence and for the effect of insects to be mitigated by wind (Witter, Johnson, Croft, Gunn, & Poirier, 2012).

Topography

Finally, we accounted for topographical covariates previously demonstrated to influence caribou (e.g. Palm et al., 2022). We derived terrain indices from 30-m resolution elevation data sets for both the US and Canada portions of the study area (Canada, 2011; USGS EROS Data Center, 2014). We accounted for elevation, 'northness' and 'eastness' representing aspect, and indices for topographic position (TPI) and terrain ruggedness (TRI). TPI values represent the difference of a cell's elevation and the average elevation of its eight neighbouring cells whereas TRI values represent the mean of the absolute differences between the value of a cell and its eight neighbouring cells (Riley et al., 1999).

3 | RESULTS

We found little support for quadratic terms in our discrete choice models. We found some support for interactive effects of insect presence and wind, but not for other covariates. Inclusion of individual identity random intercepts was strongly supported. We present results only from the behaviour choice model for 'eating' and food choice models for 'lichen' and 'shrubs' but refer readers to the Supporting information for results pertaining to other behaviours and food choices. In general, k-folds cross validation results showed high levels of predictive capacity and goodness of fit especially for the eating behaviour model (r_s = 0.61, Table 1), and in the foraging model(s), especially for shrub (r_s = 0.86) and lichen (r_s = 0.89), supporting our focus on these results.

3.1 | Behavioural choices for caribou

3.1.1 | Eating

The top model explaining the choice to eat (Tables S1 and S4) included covariates for caribou space use intensity (current year), cover of lichen, *Salix* spp. shrubs and graminoids, insects,

TABLE 1 Beta coefficients from the final discrete-choice models of factors influencing the probability of caribou choices for eating behaviour, and lichen and shrub food choice.

	Behaviour or food choice					
	Eating[a] ($n = 7869$)		**Lichen[b] ($n = 2355$)**		**Shrub[b] ($n = 2452$)**	
Covariates	**β**	**SE**	**β**	**SE**	**β**	**SE**
Intercept	**0.58**	**0.03**	**1.62**	**0.09**	**1.84**	**0.11**
FMCH space use intensity (current)	−0.03	0.02	—	—	**0.12**	**0.06**
FMCH space use intensity (cumulative)	—	—	**−0.11**	**0.05**	—	—
Lichen cover	**−0.07**	**0.02**	**0.50**	**0.07**	**−0.16**	**0.06**
Salix spp. shrub cover	**0.25**	**0.03**	**−0.23**	**0.06**	**0.47**	**0.08**
Insect presence	**−1.38**	**0.12**	−0.59	0.53	−0.59	0.40
Burns	—	—	—	—	—	—
Betula spp. shrub cover	—	—	—	—	—	—
Alnus spp. shrub cover	—	—	—	—	—	—
Graminoid cover	**−0.08**	**0.02**	**−0.48**	**0.05**	**−0.38**	**0.05**
Forb cover	—	—	**−0.20**	**0.05**	**−0.27**	**0.05**
Eastward wind speed	−0.03	0.02	**−0.19**	**0.05**	—	—
Insect × Eastward wind speed	0.24	0.14	**−1.95**	**0.74**	—	—
Northward wind speed	—	—	—	—	**−0.16**	**0.05**
Northness (aspect)	**−0.08**	**0.02**	—	—	—	—
TRI	**0.11**	**0.02**	—	—	—	—
Temperature	**−0.10**	**0.02**	—	—	**0.66**	**0.06**
Elevation	—	—	—	—	—	—
Random intercept SD[c]	0.09	—	0.32	—	0.46	—
k-folds cross validation[d]	0.64	0.06	0.89	0.02	0.86	0.10

Note: Two sets of models were developed using classified behaviour and diet data and spatial locations from GPS video-camera collars worn by female caribou ($n = 30$) of the Fortymile Caribou Herd (FMCH), Alaska, the United States and Yukon, Canada over two summers (2018 & 2019). Results of all other behaviour and food choice categories can be found in Supporting Information. Bold indicates significance at $p \le 0.05$. Model cross validation is represented by Spearman's rank correlation values and was grouped by individual.

[a] Ruminating was our reference behaviour category choices.

[b] Ground-level vegetation was our reference food category.

[c] We included random intercepts for individual caribou.

[d] Grouped-level k-folds Spearman's rank correlation evaluating model fit.

temperature, eastward wind speed, northness, terrain ruggedness (tri) and an interaction term between insects and eastward wind speed. In summer, caribou chose to eat where *Salix* spp. shrub cover was greater ($\beta = 0.25$, SE = 0.03; Table 1; Figure 3). Caribou ate where lichen ($\beta = -0.07$, SE = 0.02; Figure 3) and graminoid cover ($\beta = -0.08$, SE = 0.02; Figure 3) were low and were less likely to eat when also engaged in insect avoidance behaviours ($\beta = -1.38$, SE = 0.12; Table 1; Figure 3). Caribou were more likely to eat where temperatures were lower (mean; $\beta = -0.10$, SE = 0.02; Table 1), on south-facing slopes (northness, $\beta = -0.08$, SE = 0.02; Table 1) and where terrain was more rugged (tri, $\beta = 0.11$, SE = 0.02; Table 1). Although we removed elevation due to a strong correlation with caribou space use intensity (>±0.6), caribou were more likely to eat at lower elevations (Figure S5). Top cover of lichen and *Betula* spp. shrubs were negatively correlated ($r = -0.6$; Figure S2) but we retained other variables for the shrub model because of low collinearity and no evidence for statistical confounding. Behaviour models demonstrated moderate predictive power based on k-fold cross validation (Tables S1 and S7).

3.2 | Food choices made by caribou

We identified 7529 food items eaten by caribou and grouped food items into six categories to classify summer diets of caribou: shrubs ($n = 2452$), lichen ($n = 2355$), ground-level vegetation ($n = 698$; reference category), graminoids ($n = 499$), forbs ($n = 424$) and other food types ($n = 116$). Food choice models demonstrated higher predictive power relative to behaviour models based on k-fold cross validation (Table 1).

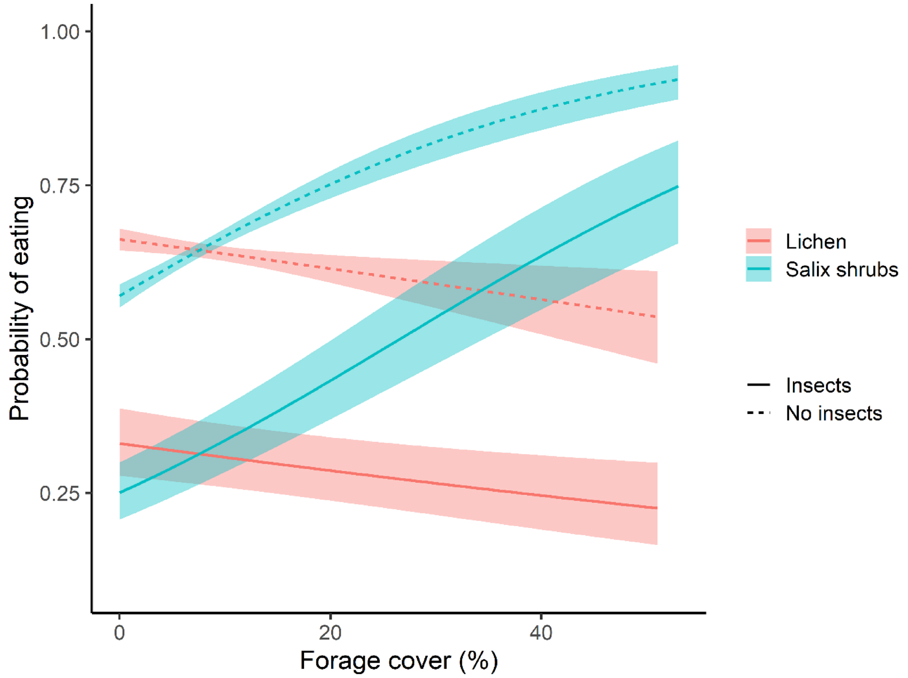

FIGURE 3 The predicted probability of caribou eating (behaviour) as a function of lichen and *Salix* spp. shrub cover relative to the reference category of ruminating for 30 adult female caribou in the Fortymile Caribou Herd (FMCH), Alaska, the United States and Yukon, Canada. We calculated the predicted probability of eating to plot the effect of each covariate on the behaviour of eating while holding the effects of other covariates at their mean. K-folds cross validation (as a measure of goodness of fit) for the eating model was high ($r_s = 0.61$).

3.2.1 | Shrubs

The top model explaining the choice to eat shrubs (Table 1; Tables S3b and S5) included covariates for caribou space use intensity (current year), top cover of lichen, *Salix* spp. shrubs, graminoids and forbs, as well as insects, temperature, northward wind speed, and temperature. Caribou were more likely to eat shrubs in summer where space use intensity of caribou increased ($\beta = 0.12$, SE = 0.06; Table 1; Figure 4), where *Salix* spp. shrub cover ($\beta = 0.47$, SE = 0.08; Figure 4) and temperatures increased (mean; $\beta = 0.66$, SE = 0.06) and where southward winds prevailed (northward winds; $\beta = -0.16$, SE = 0.05). Caribou were more likely to eat shrubs in areas of their summer range not classified by lichen ($\beta = -0.16$, SE = 0.06), graminoid ($\beta = -0.38$, SE = 0.05), or forb cover ($\beta = -0.27$, SE = 0.05). Correlation between *Salix* spp. shrubs and lichen in the probability of eating shrubs models was – 0.1 (Figure S4). The mean r_s for the shrubs food choice models was high at 0.98 (range = 0.93–1.0; SD = 0.02) and 0.86 for individual models (range = 0.64–0.99; SD = 0.10; Table S8).

3.2.2 | Lichen

The top model for feeding on lichen included covariates for caribou space use intensity (cumulative), top cover of lichen, *Salix* spp. shrubs, graminoids, and forbs, insects, eastward winds, and an interaction term for insects and eastward winds (Tables S3b and S5). Caribou were more likely to eat lichen in areas of their summer range with lower cumulative caribou space use intensity ($\beta = -0.11$, SE = 0.05; Table 1; Figure 4) and with higher lichen cover ($\beta = 0.50$, SE = 0.07; Table 1; Figure 4). Caribou were less likely to eat lichen where cover of graminoids ($\beta = -0.48$, SE = 0.05) and forbs ($\beta = -0.20$, SE = 0.05) were low and eastward winds prevailed ($\beta = -0.19$, SE = 0.05). As eastward winds and insect harassment increased, the probability of caribou eating lichen declined (Table 1; Figure S1). We found moderate correlation between lichen and *Betula* spp. shrubs in this top-ranked probability of eating lichen model (−0.5) but low correlation between lichen and *Salix* spp. shrubs (−0.2; Figure S3). The mean r_s for the lichen food choice model was high at 0.97 (range = 0.94–0.99; SD = 0.02; Table S8) and 0.89 for individual models (range = 0.58–0.99; SD = 0.11).

4 | DISCUSSION

Animal-borne video collars, in combination with advances in remote-sensing derived vegetation cover and climate data, are powerful tools for assessing fine-scale drivers of behaviour and foraging in remote regions. Using these methods, we found caribou had reduced probabilities of eating where space use intensity was higher, a proxy of spatiotemporal density and consistent with density-dependent habitat theory (Rosenzweig & Abramsky, 1985). The strongest evidence for an effect of relative space use intensity on foraging, however, came from the reduced probability of eating lichens, a key food source. However, the opposite was true for shrubs: caribou increased their probability of eating shrubs as space use intensity increased. This

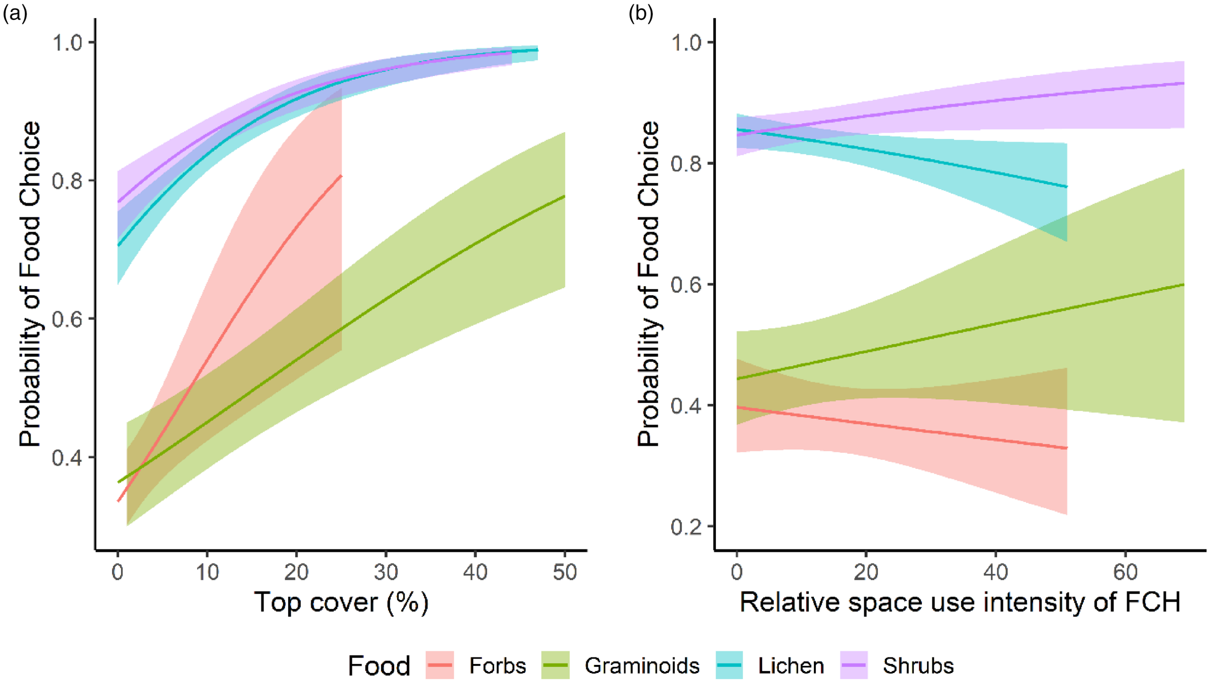

FIGURE 4 Functional response curves representing the probability of eating different food types for 30 adult female caribou from the Fortymile Caribou Herd (FMCH) in Alaska, the United States and Yukon, Canada during the summers of 2018 & 2019. Probabilities of eating food type, conditioned on being in the behaviour state of eating, are displayed as a function of that food's availability on the landscape (a) and relative space use intensity of caribou derived from GPS collar locations (b). FMCH relative space use intensity represents either current year (shrubs & graminoids) or cumulative space use intensity (lichen & forbs) specific to each food choice as detailed in Table 1.

reversed effect of space use was driven by a functional response in which the likelihood of caribou eating *Salix* spp. increased with increasing shrub cover. The evidence for density-dependent foraging on lichen is consistent with recent evidence of density-dependent declines in reproductive rates (Boertje et al., 2017). Previous studies showed density dependence in foraging behaviour, but most often used proxies like landcover class, vegetation community, or home range composition (McLoughlin et al., 2007; van Beest et al., 2014). In many of these studies, use of the putatively higher-quality patch responded to predictions of density dependence. Thus, our results suggest density-dependent responses observed at larger scales are consistent with fine-scale density dependence in foraging. Further, fine-scale foraging behaviour operated in a density-dependent fashion consistent with theory. As competition between conspecifics increased, the probability of caribou eating lichen declined in a manner consistent with predictions from overgrazing (Figure 4; Table S3b). Lichens are sensitive to overgrazing from caribou (e.g. Klein, 1987; Manseau et al., 1996; Rickbeil et al., 2015). Past studies documented depletion of lichens following phases of high-densities of caribou that were followed by population declines (Klein, 1968; Mallory et al., 2020; Messier et al., 1988; Miller & Gunn, 2003). This pattern is especially relevant for lichen because they require decades to recover from overgrazing (Crittenden, 1999; Henry & Gunn, 1991). For the FMCH, whose summer and winter ranges have high overlap, grazing and trampling during summer will also affect lichen abundance on their winter range. Long-term declines in overwinter lichen can lead to declining nutritional conditions, reduced overwinter calf survival, population declines, and range shifts for caribou (Ferguson et al., 2001; Rickbeil et al., 2017).

Our results suggest caribou prefer eating shrubs over lichens in summer, even where lichen cover was higher (Table S1). Indeed, caribou chose to eat where *Salix* spp. cover was greater (Figure 3; Maps S1–S4). This outcome is intuitive given the greater nutritional value (Klein, 1990) of shrubs during summer. With higher nutritional demands for reproduction in summer (White et al., 2013), caribou expand their diet, shifting to include high nitrogen content shrubs and other species (Boertje, 1981; Ehlers et al., 2021; Skoog, 1956). In contrast to declining foraging on lichen with increased space use intensity, the probability of caribou eating shrubs increased with space use intensity (Figure 4; Table S3b). Shrubs are more tolerant of and can rapidly recover after excessive grazing (Klein, 1987; van der Wal, 2006). Our results support the idea of increased resilience of shrubs to density-dependent effects of caribou grazing (Table 1; Figure 4) and highlight potential risks of overgrazing to sensitive species, like lichens, in a changing global climate.

In a global meta-analysis, (Cornelissen et al., 2001) suggested that climate-changed induced increases in vascular plants may also contribute to lichen declines. Reductions in lichen cover resulting from indirect competition caused by shrub expansion (Myers-Smith et al., 2011) and/or disturbance may eventually lead to a reduced ecological carrying capacity (*K*) for caribou (Joly et al., 2009). Despite lichens being a less preferred forage in summer, they remain the second most consumed forage in the FMCH despite their nutritionally poor, but energy rich composition (Ehlers et al., 2021;

Webber et al., 2022). So, although shrub expansion could benefit caribou as an abundant high-quality summer food, it will likely come at the cost of future declines in lichen, due to disturbances (e.g. fire) potentially resulting in long-term consequences for reproduction and survival (Boertje, 1990; Palm et al., 2022). The nutritional quality of expanding shrub communities for caribou will also strongly depend on which species of shrubs expand. We speculate the evidence we observed for the drivers of fine-scale foraging in summer will only be exaggerated for caribou in winter due to reduced diversity and availability of quality foods.

GPS video collars offer a way to quantify functional responses for a wider range of species and across diverse ecosystems at scales relevant for landscape and population management (e.g. Senft et al., 1987; Figure 4). Although the link between the probability of foraging and actual intake rate remains unknown (e.g. Thompson Hobbs et al., 2003), diet results collected from video collars and those from faecal microhistological studies suggest the two are correlated (Ehlers et al., 2021). Further, maps depicting probability of eating certain food types (e.g. Maps S1–S4) can identify high-quality foraging habitats for conservation efforts at large landscape scales.

While our discrete-choice models provided many advantages, there were some necessary limitations. First, we acknowledge the challenge of interpreting conditional probabilities of behaviours and/or foraging on specific food types in comparison to a reference category (Figure 2; McFadden, 1981). Another inherent challenge is testing predictions of density-dependent habitat theory from relative space use intensity. Future studies could use our approach after a decade of population change to test if predictions from space use intensity are consistent with actual changes in abundance. Moreover, weighting caribou space use intensities with annual population estimates did not change our coefficient estimates, confirming broad support for our interpretation of spatial density dependence. Additionally, future studies should, if possible, include top-down effects of the landscape of fear, which could have large effects on the behavioural choices of large ungulates (Chamaillé-Jammes et al., 2014).

These challenges do not limit the valuable insights provided into documenting fine-scale, density-dependent foraging for wild herbivores across remote subarctic and arctic regions. By investigating not only where, but why caribou choose to eat the foods they do, we found that fine-scale choices are being driven by density-dependent, density-independent, and biotic factors. Our results highlight that caribou may have increased access to shrubs but decreased access to lichen in areas of their range with high space use intensities. Finally, in a rapidly changing Arctic, our results provide the basis for understanding the effects of how changes in caribou density and cover of critical summer forages differentially affected by climate change will affect the mechanisms of ungulate foraging in the future.

AUTHOR CONTRIBUTIONS

Libby Ehlers, Mark Hebblewhite, Jim Herriges, Torsten Bentzen, Mike Suitor and Josh Millspaugh conceived the ideas and designed methodology; Libby Ehlers, Jim Herriges, Torsten Bentzen and Mike Suitor collected the data; Libby Ehlers analysed the data; Libby Ehlers led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xwdbrv1n5 (Ehlers et al., 2024).

STATEMENT ON INCLUSION

Our study included a number of authors from different countries, including scientists based in both the United States and Canada where the study was conducted. All authors were engaged early on with the research and study design to incorporate diverse sets of perspectives they represented. Whenever relevant, literature published by scientists from the region was also cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Beta coefficients from the final discrete-choice models of factors influencing the probability of caribou behavior compared to the reference category of ruminating.

Table S2: Beta coefficients from the final discrete-choice models of factors influencing the probability of caribou ruminating as a behavior as compared to an alternate reference category of traveling.

Table S3a: Average monthly cover values (%; mean and std dev.) for the four of the preferred foraging choices available to caribou of the Fortymile Caribou Herd (FMCH) outfitted with GPS video camera collars ($n = 30$) where individuals were observed eating (behavior choice = eating) during the summers of 2018 and 2019.

Table S3b: Beta coefficients from the final discrete-choice models of factors influencing the probability of caribou food choices as compared to the reference category of ground-level vegetation.

Table S4: Comparison of discrete choice (GLMER) regression models for describing behavior choices for female caribou ($n = 30$) of the Fortymile Caribou Herd, Alaska, USA and Yukon, Canada.

Table S5: Comparison of discrete choice (GLMER) regression models for describing food choices for female caribou ($n = 30$) of the Fortymile Caribou Herd, Alaska, USA and Yukon, Canada.

Table S6: Beta coefficient table for discrete models for ‘other’ behavior and food choices for caribou of the Fortymile Caribou Herd, Alaska, USA and Yukon, Canada.

Table S7: Spearman's rank correlation values and summaries for each final ‘behavior choice’ model using a discrete-model approach for caribou of the Fortymile Caribou Herd of Alaska, USA and Yukon, Canada.

Table S8: Spearman's rank correlation values and summaries for each final ‘food choice’ model using a discrete-model approach for caribou of the Fortymile Caribou Herd of Alaska, USA and Yukon, Canada.

Table S9: Marginal rates of substitutions (MRS) table for behavior choices made by caribou as assessed during our discrete choice analysis.

Table S10: Marginal rates of substitutions (MRS) table for food choices made by caribou as assessed during our discrete choice analysis.

Table S11: Summary of animal locations used to estimate annual occurrence distributions (ODs) using Brownian bridge movement models for the Fortymile Caribou Herd (FMCH) across Alaska and Canada.

Table S12: Summary of animal locations used to estimate seasonal occurrence distributions (ODs) using Brownian bridge movement models for the Fortymile Caribou Herd (FMCH) across Alaska and Canada.

Table S13: The mean proportion of top cover (%) at each location caribou of the FMCH were observed eating (behavior; $n = 7869$ observations) for each month of the summer season (May = 5, June = 6, July = 7, Aug = 8, Sept = 9).

Figure S1: Interaction plots assessing relationships between the probability of engaging in the behavior of eating (A; all forage types included) or eating lichen (B) and the biotic and abiotic factors of insect harassment and wind speed (m/s).

Figure S2: Correlation plot in discrete choice analysis of eating ($n = 7869$) as an observed behavior choice.

Figure S3: Correlation plot in discrete choice analysis of lichen ($n = 2355$) as an observed food choice.

Figure S4: Correlation plot in discrete choice analysis of shrubs ($n = 2452$) as an observed food choice.

Figure S5: The probability of eating during summer for caribou as it related to elevation (m).

Figure S6: Population estimates for the FMCH over 12 years (2009–2022).

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