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Research Article

Delineating seasonal shifts in reindeer habitat and diet selection by integrating GPS telemetry and stable isotope analysis

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Seasonal changes shape herbivore behaviour by altering forage availability and habitat conditions; however, few studies integrate diet and habitat selection data across temporal scales. This study uses seasonality as a unifying framework to combine fine-scale GPS-based habitat selection data with broader-scale dietary information from stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of hairs in semi-domesticated reindeer *Rangifer tarandus tarandus*. Thresholds introduced within this framework detect seasonal shifts in habitat and diet selection and classify foraging strategies along a specialist–generalist continuum. Despite individual variability, most individuals exhibited pronounced seasonal changes between spring/early summer (SES) and late summer/autumn (LSA), consistent with generalist foraging strategies. Habitat selection models revealed reduced avoidance of rugged terrain and increased use of mires and bogs from SES to LSA. Concurrently, isotopic enrichment and niche expansion reflected a dietary shift from $\delta^{15}N$- and $\delta^{13}C$-depleted plants (e.g. lichens, shrubs, deciduous vegetation) to more enriched forage types such as sedges, grasses, horsetails, and mushrooms. We assessed whether individual-level shifts in diet and habitat use were linked and found an inverse correlation between the shifts in terrain ruggedness avoidance and dietary change in approximately 67% of individuals, suggesting that behavioural flexibility facilitates seasonal transitions. By integrating spatial and isotopic data, this study overcomes the limitations of single-method approaches and provides a more nuanced understanding of the seasonal foraging dynamics of a keystone Arctic and boreal ungulate. The findings highlight the plasticity of reindeer foraging within a variable environment and suggest a capacity to respond to environmental changes. This framework also offers broader applications for investigating behavioural responses and ecological strategies in other herbivores facing climate-driven habitat shifts.

Keywords: Arctic, diet, Finland, GPS-tracking, *Rangifer tarandus tarandus*, resource selection, seasonal shifts, semi-domesticated reindeer, stable isotope, trophic niche

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Introduction

Seasons play a crucial role in regulating the rhythms, lifecycles and behaviours of many species (Steltzer and Post 2009, Simmonds et al. 2025). However, climate change has altered the timing, duration and characteristics of seasons, particularly in northern environments (Reyes-Fox et al. 2014, Wang et al. 2021). Longer summers have led to phenological mismatches and changes in forage quality, quantity, and accessibility, directly influencing herbivore habitat use and diet selection (Bintanja and Van Der Linden 2013, Beard et al. 2019, Twining et al. 2022). As a result, generalist species and those with behavioural or niche plasticity may be better equipped to buffer or adapt to the effects of seasonal creep, thereby mitigating potential consequences for fitness and survival (Hallam and Harris 2023, Dwinnell et al. 2024, McKibben and Frey 2025). Nevertheless, it remains insufficiently understood whether the foraging strategies and diets of generalist herbivores are truly plastic enough to facilitate adaptation to changing seasonality.

Herbivore foraging ecology investigations traditionally follow the framework of classic optimal foraging theory (OFT; Pyke et al. 1977), which distinguishes between optimal diet, i.e what animals eat (Spitzer et al. 2020), and optimal patch or habitat, i.e where they go (Beumer et al. 2020). Technological advances in GPS telemetry (Gurarie et al. 2016, Abrahms et al. 2021) and dietary investigation methods (Nielsen et al. 2018, Hobson 2023) have greatly enhanced the availability of fine-scale data on animal movements and diets. However, many dietary investigation methods, such as DNA metabarcoding or microhistology of stomach contents or faeces, provide only a snapshot of diet immediately prior to sampling. Moreover, most foraging ecology studies overlook the temporal and spatial dimensions of foraging strategies and shifts, as well as the effects of cumulative foraging events. This gap is due to the challenges in gathering high-resolution data on the type, quantity, quality, and distribution of resources in the landscape and the diet over time, compounded by financial and logistical constraints (Iversen et al. 2014, Novak and Tinker 2015, Szigeti et al. 2019).

Stable isotope analysis (SIA) has been widely used to determine the trophic niches and diets of populations and individuals across varying temporal and spatial scales (Rogers et al. 2020, Hiltunen et al. 2022, Massé et al. 2023). Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) from plants consumed by herbivores are assimilated into different tissues at varying rates due to isotope discrimination processes as well as growth and tissue turnover (Tieszen et al. 1983, Dalerum and Angerbjörn 2005, Ben-David and Flaherty 2012). For example, hairs grow progressively from the root, capturing dietary stable isotopes along the shaft (Schwertl et al. 2003, Mosbacher et al. 2016, Rogers et al. 2020), comparing these values across sections allows researchers to quantify the temporal stability or variability of an individual's diet through isotopic niche trajectories (Bond et al. 2016, Sturbois et al. 2022, Li et al. 2024).

Combining stable isotope measurements with GPS tracking has provided valuable insights into the relationships between diet, migration patterns, habitat use and foraging patch selection across various taxa (Rogers et al. 2015, Zeppelin et al. 2015, Micheli-Campbell et al. 2017, Robillard et al. 2021). However, the few herbivore studies that have combined these methods have focused primarily on group assignment or validating observational data (Cerling et al. 2006, Walter et al. 2010, Hansen et al. 2019), leaving the direct integration of diet and landscape use underutilised in ungulate research. Consequently, the influence of ungulate movement and foraging strategies on diet composition and isotopic niche dynamics in heterogeneous, seasonal landscapes remains poorly understood. Addressing this gap would enhance our understanding of key ecological processes such as resource partitioning, seasonal habitat preferences, and dietary variability. This study leverages the integration of stable isotope analysis and GPS tracking to investigate seasonal shifts in herbivore diet and habitat selection, using semi-domesticated reindeer *Rangifer tarandus tarandus* as the study species.

Reindeer and caribou (*Rangifer* spp.) exhibit considerable adaptability in response to seasonal and environmental changes due to their flexible foraging habits (Clark-Wolf et al. 2025, Simmonds et al. 2025). As mixed feeders, they consume hundreds of plant species (Åhman and White 2018), alternating between selective specialists when preferred plants are abundant and generalists when plant quality, diversity, or biomass declines (Skogland 1984, Nieminen and Heiskari 1989, Iversen et al. 2014). Both habitat and foraging patch selection are influenced by the availability and diversity of palatable, nutrient-rich plants and the energetic costs of resource acquisition (Pape and Löffler 2015, Barboza et al. 2018, Richert et al. 2021, Romtveit et al. 2021). Beyond diet, habitat selection and movement are also influenced by predator avoidance, particularly during calving, and the avoidance of harassment by blood-sucking and parasitic insects in summer (Johnson et al. 2021, 2022). The dynamic interactions between reindeer, their environment, and seasons influence landscape use, foraging behaviour, and diet selection, ultimately affecting their fitness and survival, highlighting the need for high-resolution integrative studies to understand how these factors shape herbivore responses to environmental change (Post and Stenseth 1999, Mallory and Boyce 2018). Within populations, individuals may follow different strategies, with some maintaining relatively stable habitat and diet preferences (specialists), while others are generalists, varying their selection of habitat, diet or both seasonally (Bolnick et al. 2003, Araújo et al. 2011, Powell and Taylor 2017, McKibben and Frey 2025). This variation in individual strategies may influence how reindeer populations respond to environmental change and resource fluctuations, highlighting the importance of studying selection patterns across multiple scales.

In this study, we aim to quantify seasonal shifts in reindeer foraging behaviour by integrating two datasets reflecting

Table 1. Predicted seasonal habitat and dietary selection patterns in semi-domesticated reindeer, based on a framework of four foraging strategies positioned along a specialist–generalist continuum. [a]Habitat selection parameters considered: RSF odds ratio (OR) classifications. [b]Diet selection parameters considered: Isotopic niche trajectories, trajectory angles (θ_i) and Rao's spacing statistic. Population isotopic niche ellipses – SEA_B.

Foraging strategy	Habitat selection (HS)[a]	Diet selection (DS)[b]
Specialist habitat and diet selection strategy	Specialist (HS_S)	Specialist (DS_S)
Reindeer are selective feeders (dietary specialists) as their foraging preferences remain consistent throughout the seasons; however, they exhibit little to no change in their habitat selection and usage (habitat specialists).	No seasonal differences	No seasonal differences
Specialist habitat selection and generalist diet selection strategy	Specialist (HS_S)	Generalist (DS_G)
Reindeer are dietary generalists, as their foraging preferences change with the seasons. However, they remain habitat specialists, with little to no change in their habitat selection and usage.	No seasonal differences	Seasonal differences
Generalist habitat selection and specialist diet selection strategy	Generalist (HS_G)	Specialist (DS_S)
Reindeer are selective feeders (dietary specialists) as their foraging preferences remain consistent throughout the seasons; however, their habitat selection and usage change.	Seasonal differences	No seasonal differences
Generalist habitat and diet selection strategy	Generalist (HS_G)	Generalist (DS_G)
Reindeer individuals are dietary generalists as their forage preferences change between the seasons, and their habitat selection and usage change.	Seasonal differences	Seasonal differences

different spatial and temporal scales, i.e. fine-scale GPS-based habitat selection and broader-scale stable isotope-derived diet selection. We hypothesised that individuals may adopt one of four combined habitat–diet strategies, each reflecting a different position along the specialist–generalist continuum, as defined by a structured framework with specific predictions for seasonal shifts in habitat and diet selection (Table 1). To test these predictions, we analyse the seasonal changes in habitat selection and diet composition (Table 2) and then assess the hypotheses based on the results. This approach provides insight into how reindeer adapt to seasonal environmental changes and whether the population consists of individual specialists, generalists, or a mix of both. Finally, we investigate the extent to which the shifts in habitat and diet selection are interconnected. In this way, we aim to evaluate how concurrent changes in habitat use and diet across seasons enable reindeer to adapt to seasonal changes in their pasture environment.

Material and methods

Study area and species

The study was conducted from February to October 2019 in the Kaldoaivi *Gálddoaivi* reindeer herding district in northern Finland (69°47′N, 27°36′E; Fig. 1a), which covers 2478 km². Kaldoaivi borders Finnmark County, Norway (Fig. 1b) and forms part of the *Sámi* indigenous homeland *Sápmi*. While English terminology is primarily utilised, *Sámi* terms are acknowledged in parentheses. The herding of semi-domesticated reindeer *R. t. tarandus* is culturally and economically important to the *Sámi* (Sarkki et al. 2016). Kaldoaivi is fenced but not subdivided into separate summer and winter grazing areas, allowing reindeer to roam freely across the entire district year-round.

The landscape of the study area is hilly and primarily composed of mires, mountain birch *Betula pubescens* ssp. *czerepanovii* forests, tundra heaths and rocky or gravelly terrain. Small patches of pine forest *Pinus sylvestris* are confined to the Utsjoki River *Ohcejohka* valleys, with smaller pockets scattered across the district. The elevation ranges from 10 to 446 m a.s.l. (Kumpula et al. 2019). Located north of the Arctic Circle, the area experiences midnight sun (16 May–27 July) and polar night (26 November–16 January). Winters are cold (mean January temperature: −14.3°C), and summers are mild (mean July temperature: 13.3°C), with snow cover lasting for six months, from mid-October to mid-May (Finnish Meteorological Institute 2023). In 2019, snow melted on 30 April and 10 May at the Nuorgam and Kevo Sub-Arctic Research Station weather stations, respectively. Annual precipitation was relatively low, totalling 376 mm (Finnish Meteorological Institute 2023, Supporting information).

Reindeer collaring and hair sampling

Reindeer in Kaldoaivi are rounded up and handled for management purposes twice annually, in mid-to-late winter (February/March) and autumn (October/November), providing opportunities for collaring and sample collection. In February 2019, 15 adult female reindeer were fitted with Ultracom Poro GPS M5 collars (Ultracom Oy, Oulu, Finland) at the Skalluvaara *Skállovárri* roundup site (Fig. 1c). The GPS collars recorded locations at a frequency of four locations per day. Collars were removed during autumn 2019 (n = 13) and spring 2020 (n = 2) roundups, and hair samples were collected from the rump next to the tail and stored in paper bags (Mosbacher et al. 2016). All collars were sent to Ultracom Oy (Oulu, Finland) for the data to be downloaded.

Sample preparation and stable isotope analysis

Reindeer hair samples were processed for stable isotope analysis (SIA) following established protocols in the literature (Rogers et al. 2020, Hiltunen et al. 2022, Massé et al. 2023). Samples were washed overnight in 2:1 chloroform/methanol (67/33, v/v) on an orbital shaker (180 oscillations minute^{-1}) to remove sebum lipids. They were then rinsed with fresh solvent, ethanol (twice), and distilled water (twice) and

Table 2. Summary of the results consistent with the framework presented in Table 1, which outlines four foraging strategies positioned along a specialist–generalist continuum. The predictions address seasonal differences in habitat and dietary selection, assuming that the semi-domesticated reindeer in this study adopted one of the four proposed foraging strategies between the two seasons (spring/early summer [SES] and late summer/autumn [LSA]). Seasonal patterns of habitat selection (HS) are described using classified odds ratios (OR) derived from resource selection functions (RSFs; Johnson et al. 2006, Avgar et al. 2016, Fieberg et al. 2021), based on GPS location data collected every six hours. Seasonal dietary selection (DS) patterns/differences are described using isotopic niche trajectories (individual level) and ellipses (population level; Jackson et al. 2011, Bond et al. 2016, Costa-Pereira et al. 2019) based on hair isotope values ($\delta^{13}C$, $\delta^{15}N$). [a]An odds ratio (OR) of 1 in an RSF indicates random selection (RS), while values < 1 represent avoidance (−) and values > 1 indicate preference (+). [b]Trajectory angle (θ_i) indicates the direction of dietary shifts. Directionality was assessed using Rao's spacing statistic (U), which compares the observed angular spacing to that expected under uniformity. For uniformity, $U < U_{0.05}$, while for directionality, $U > U_{0.05}$. [c]Significant differences ($p < 0.05$, *) in SEAB between seasons were determined by comparing the proportions of posterior ellipses (PP), considered significant when $PP \geq 0.95$ or $PP \leq 0.05$.

		Prediction (change from SES to LSA)		
Selection parameter		Specialisation	Statistics	Support
Habitat selection	RSF odds ratios (OR)[a]	Specialist (HS_S)	+ → + − → −	No
		Generalist (HS_G)	+ ↔ − + ↔ RS − ↔ RS RS → RS	Yes (Supporting information)
Diet selection	Trajectory angle (θ_i)[b]	Specialist (DS_S)	$U > U_{0.05}$	No
		Generalist (DS_G)	$U < U_{0.05}$	Yes ~ $U = 166.21 < U_{0.05} = 169.09$
	Population SEA_B	Specialist (DS_S)	SES ≈ LSA PP[c]: 0.05–0.95	No
		Generalist (DS_G)	SES ≠ LSA PP[c]: *	Yes ~ 0.20 ≠ 0.48 $PP_{SES<LSA} = 0.017$

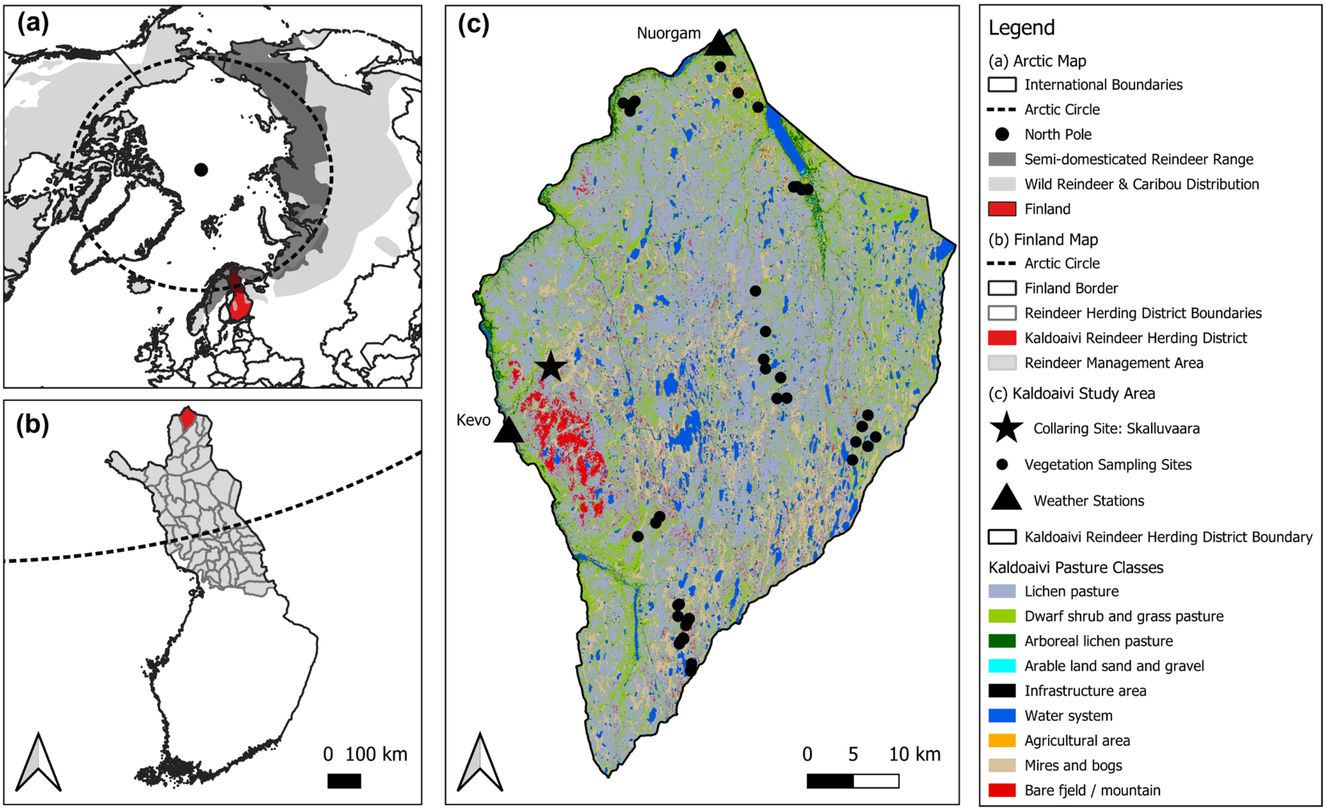

Figure 1. Location of the study area. (a) Map of the circumpolar Arctic showing the distribution of semi-domesticated and wild reindeer, with Finland delineated with a red polygon. (b) Map of Finland showing the reindeer management area and the boundaries of all 54 reindeer herding districts, with the Kaldoaivi reindeer herding district highlighted with a red polygon. (c) Map of the study area showing pasture classes. Skalluvaara, the reindeer roundup site where the reindeer collaring took place, is marked with a black star. Black triangles indicate the locations of the Kevo and Nuorgam meteorological stations.

subsequently dried at 50°C for 24 h. The longest whole hairs (15–20 sample^{-1}) were cut into 2 cm sections using a surgical scalpel. Of 13 samples, only 12 had both follicle (A) and tip (B) sections, and the hair sections of each reindeer were pooled accordingly. Hair sections (0.8–1.2 mg) were weighed into 5 × 9 mm tin capsules (Elemental Microanalysis Ltd).

Samples were analysed at the Environment and Natural Resources Institute Stable Isotope Laboratory at the University of Alaska Anchorage (www.uaa.alaska.edu/enri/labs/sils). $\delta^{13}C$ and $\delta^{15}N$ values (‰) were calibrated against internal standards (BWBII keratin, peach leaves, moose *Alces alces*, and three-spined stickleback *Gasterosteus aculeatus*) and referenced to the international standards of Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 (air) for $\delta^{15}N$. Concentrations of the heavy isotopes (^{13}C and ^{15}N) are reported using the standard delta notation (δ) in parts per thousand relative to an international standard (Eq. 1):

$$\delta_{\text{sample}} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, 0 \qquad (1)$$

where δ_{sample} is the stable isotope ratio of $\delta^{13}C$ or $\delta^{15}N$ in the sample, R_{sample} and R_{standard} are the molar ratios of heavy to light isotopes ($^{13}C/^{12}C$; $^{15}N/^{14}N$) in the sample or the reference standard, respectively (Fry 2006, Michener and Lajtha 2007). The sample analytical error was ± 0.1‰ for both C and N.

Statistical analysis of data

All statistical analyses were conducted in R ver. 4.2.1 (www.r-project.org) using RStudio (ver. 2023.03.1+446). The Supporting information provides a schematic overview of the complete analytical workflow, from processing reindeer hair samples and GPS data to generating datasets for the habitat–diet shift models.

Categorisation of the data

Based on previous caribou studies (Drucker et al. 2010, Macbeth 2013), the follicle section (A) of the hair represents diets from July to October (late summer to autumn), while the tip (B) reflects diets from April to June (spring to early summer). Of the 15 collared reindeer, only 12 had complete stable isotope and GPS datasets available for further analysis. GPS data were grouped into two seasonal periods: spring/early summer (SES; May–June; $\bar{n}$ = 243 locations individual^{-1}) and late summer/autumn (LSA; July; $\bar{n}$ = 113 locations individual^{-1}; Supporting information) to best align with the dietary periods represented by the hair sections. The final GPS dataset was rechecked for outliers and anomalies.

Resource selection functions (RSFs) and habitat usage

Resource selection function models (RSFs) were fitted for each season and individual using the R package 'amt' (ver. 0.2.1.0; Fieberg et al. 2021), according to Uboni et al. (2017). Each GPS location (used habitat; case = TRUE) was paired with 15 randomly selected locations within the Kaldoaivi district (available habitat; case = FALSE). The binomial variable, case, served as the response variable in our logistic regression models fitted using the R function *glm* by specifying a binomial error distribution and a logistic link function (R package 'lme4' ver. 1.1-32; Bates et al. 2015).

Habitat and topographic predictor variables, known drivers of reindeer habitat selection and forage distribution (Nellemann and Fry 1995, Kumpula et al. 2006, Sundqvist et al. 2019), were extracted from the Finnish GIS coverages of elevation (elev), terrain ruggedness (rug), vegetation type (past) and normalised difference vegetation index (NDVI). Vegetation coverage (30 m resolution) included nine pasture classes (Kumpula et al. 2006): lichen pasture (LP), dwarf shrub and grass pasture (DSGP), arboreal lichen pasture (ALP), arable land, sand and gravel (ALSG), infrastructure area (IA), water system (WS), agricultural area (AA), mires and bogs (MB) and bare fell/mountain (BFM).

Elevation (meters above sea level) and terrain ruggedness (index representing the absolute difference between the elevation of a grid cell and the mean of the eight surrounding cells; Riley et al. 1999) were derived from a 10 m digital elevation model (DEM; National Land Survey of Finland 2019). NDVI values, based on red and near-infrared (NIR) reflectance ratios (Pettorelli et al. 2005) derived from the 2019 Sentinel-2 imagery, were obtained from terraPulse Inc.. Maximum monthly NDVI values were calculated at a 10 m resolution for each GPS location and month combination. All continuous covariates were standardised (mean = 0, SD =1) to improve the numerical stability of parameter estimation. Model selection was performed using a forward selection process, with model performance evaluated using the Bayesian information criterion (BIC; Pohle et al. 2017, Beumer et al. 2020) and the p-values.

Regression coefficients (βs) and log odds ratios (OR) for each habitat variable k (k={elev, rug, past, NDVI}) were extracted from the selected RSF models for each individual i (i = 1, …, 12) and season (Supporting information). Coefficients for habitat variables not included in the selected RSF models were assigned a value of zero. The percentage of females per season ($\%_{\text{RSF\_Pop } i}$) preferring or avoiding each resource was calculated based on the coefficients included in the selected RSF models. Seasonal change in habitat selection by each reindeer ($\Delta\beta_{i,k}$; shift coefficient) was calculated by subtracting $\beta_{\text{SES } i,k}$ from $\beta_{\text{LSA } i,k}$ (Supporting information). Home range size (HR_i, km^2) and the proportion of each pasture class used ($\text{Prop}_{\text{Past } i}$) for each individual and season were extracted from the RSF models to calculate the seasonal changes in home range size (ΔHR_i) and pasture class use ($\Delta\text{Prop}_{\text{Past } i}$). Additionally, mean seasonal home range sizes were tested for significant differences using a paired Wilcoxon signed-rank test ($\alpha = 0.01$). Odds ratios (OR) were classified as OR < 1 (avoidance, −), OR = 1 (random selection, RS), or OR > 1 (preference, +). Avoidance indicates that the habitat variable in question is used less than expected under random habitat selection, while preference means greater than expected use.

Isotopic niches and trajectories

Mean $\delta^{13}C$ and $\delta^{15}N$ values from the reindeer hair sections were tested for significant seasonal differences using a paired Wilcoxon signed-rank test ($\alpha = 0.01$). These values were used to reconstruct the seasonal isotopic niche ellipses using the 'SIBER' package (stable isotope Bayesian ellipses in R; ver. 2.1.6; Jackson et al. 2011). Standard ellipse areas (SEA_C), corrected for small sample size and representing a 95% probability of containing sampled parameters, were plotted with $\delta^{13}C$ and $\delta^{15}N$ values in bivariate δ-space.

Bayesian standard ellipse area (SEA_B) estimates, generated from 10^4 replicates, were used to test for seasonal differences by comparing the proportion of posterior ellipses that differed (PP), with differences considered significant if $PP \geq 0.95$ or $PP \leq 0.05$. Bayesian credible intervals derived from SEA_B were also compared to assess seasonal differences in niche breadth (Cheeseman et al. 2021), and the overlap of the 95% prediction ellipses between seasons was calculated.

Individual isotopic niche trajectories (distance, angle and direction; Supporting information) between hair section isotopic values were calculated using the 'circular' R package (ver. 0.4-93; Agostinelli and Lund 2017) to assess seasonal dietary shifts in the reindeer (Costa-Pereira et al. 2019, Agostinho et al. 2021). Two key properties of niche trajectories in bivariate isotopic δ-space were calculated using vector arithmetic (Supporting information; Eq. 2–3): trajectory length (i.e magnitude of change, X_i) and direction (i.e angle of change, θ_i). The niche trajectory vector was defined between the $\delta^{13}C$ and $\delta^{15}N$ values in B (tip) and A (follicle) sections, with trajectory length (X_i) quantified as the Euclidean distance between the B ($B_i\delta^{13}C$, $B_i\delta^{15}N$) and A ($A_j\delta^{13}C$, $A_j\delta^{15}N$) sections of hair for each individual i ($i = 1, \ldots, 12$):

$$X_i = \sqrt{\left(A_i\delta^{13}C - B_i\delta^{13}C\right)^2 + \left(A_i\delta^{15}N - B_i\delta^{15}N\right)^2} \tag{2}$$

The angle of change for individual i (θ_i) is measured as the positive counterclockwise angle between the positive x-axis ($\delta^{13}C$) and the vector representing the niche trajectory (Eq. 3).

$$\theta_i = \tan^{-1}\left(\frac{\left(A_i\delta^{15}N - B_i\delta^{15}N\right)}{\left(A_i\delta^{13}C - B_i\delta^{13}C\right)}\right) \tag{3}$$

Since trajectory angles are circular variables ranging from 0 to 2π radians, they cannot be used directly in linear mixed effects models. Instead, sine ($\sin\theta_i$) and cosine ($\cos\theta_i$) transformations are used to represent vertical ($\delta^{15}N$) and horizontal ($\delta^{13}C$) changes. Trajectory length quantifies the magnitude of the diet shift, while trajectory angle indicates the direction of change (Dalerum and Angerbjörn 2005).

To test whether the observed circular distribution of reindeer isotopic trajectory angles differed from random expectations, 10 000 null trajectories were generated. For each individual, the starting point was fixed, and an endpoint was randomly assigned from the pool of observed endpoints without replacement (Costa-Pereira et al. 2019, Agostinho et al. 2021). Directionality was assessed using Rao's spacing statistic (U), which compares the observed angular spacing to that expected under a uniform circular distribution (Pewsey et al. 2013).

Linking seasonal shifts in habitat and diet selection

To link seasonal shifts in habitat and diet selection, it is first necessary to confirm that such shifts occurred and that reindeer adopted a generalist habitat–diet foraging strategy (Table 1). This was evaluated by comparing observed changes against predefined thresholds for habitat and diet selection that distinguish generalists from specialists (Table 2). The thresholds were based on habitat selection OR classifications and diet selection metrics: Rao's spacing statistic (U) and the proportion of SEA_B posterior ellipses that differed (PP). An individual was classified as a habitat selection generalist (HS_G) if seasonal shifts occurred in one or more OR: for example, from preference to avoidance (+ → −), preference to random selection (+ → RS), or avoidance to random selection (− → RS), and vice versa (Table 2, Supporting information). Random selection in both seasons (RS → RS) was also considered indicative of generalism. Diet selection generalism (DS_G) at the population level was defined by a random distribution of trajectory angles (θ_i), indicated by an observed Rao's A statistic below the critical value at the 95% confidence level ($U < U_{0.05}$; Li et al. 2024) and by a significant difference in the size of SEA_B between seasons ($PP \geq 0.95$ or $PP \leq 0.05$).

The habitat selection shift coefficients ($\Delta\beta_{i,k}$; Supporting information) for each habitat variable were then used as candidate predictor variables in linear regression models, fitted using the *lm* function in R. The response variables (X_i, $\sin\theta_i$, $\cos\theta_i$; Supporting information) were analysed individually using simple single-predictor models to explore all possible combinations of the candidate explanatory variables ($\Delta\beta_{i,k}$), while preventing over-parameterisation due to the small sample size ($n = 12$). Model performance was evaluated using the Akaike information criterion (AIC) corrected for small sample size, AICc ('cAIC4' R package ver. 1.0; Säfken et al. 2021), adjusted R^2 values, p-values and the 95% confidence intervals derived from the sensitivity analysis. Models with positive R^2 values, normally distributed residuals with constant variance and $\Delta AICc < 2$ from the best model were considered (Burnham and Anderson 2004).

Sensitivity analysis of predictor uncertainty

To account for uncertainty arising from the RSF regression coefficients on the Δβs used as predictors in the linear regression models, we conducted a sensitivity analysis. Each model was refitted with predictor values ($\Delta\beta_{i,k}$) randomly drawn from individual-specific distributions that reflected the uncertainty associated with each $\Delta\beta_{i,k}$. Since $\Delta\beta_{i,k}$'s represent the differences between season-specific $\beta_{i,k}$'s ($\beta_{LSA\ i,k}$, $\beta_{SES\ i,k}$), their variance $Var(\Delta\beta_{i,k})$ is equal to $Var(\beta_{LSA\ i,k}) + Var(\beta_{SES\ i,k}) + 2Cov(\beta_{LSA\ i,k}, \beta_{SES\ i,k})$. While the variances of $\beta_{i,k}$'s were estimated from the RSF models (as standard errors), analytical estimates of the covariance were not available. Therefore, we approximated the covariance by assuming that the population-level correlation between $\beta_{\mathrm{LSA}\ i,k}$ and $\beta_{\mathrm{SES}\ i,k}$ reflects the individual-level correlation between the same parameters.

To implement this, a population-level correlation matrix, $\boldsymbol{R}$, was constructed for the season-specific betas based on empirically derived correlation estimates (calculated across individuals) and then converted $\boldsymbol{R}$ to a covariance matrix, $\boldsymbol{C}_i$, separately for each individual i using the RSF-derived SE($\beta_{\mathrm{LSA}\ i,k}$) and SE($\beta_{\mathrm{SES}\ i,k}$) (i.e RSF-derived standard errors of the βs for individual i in habitat variable k) in the conversion:

$$\boldsymbol{C}_{i,k} = \boldsymbol{D}_{i,k}\boldsymbol{R}\boldsymbol{D}_{i,k} \qquad (4)$$

where $\boldsymbol{D}_{i,k}$ is a diagonal matrix including SE($\beta_{\mathrm{LSA}\ i,k}$) and SE($\beta_{\mathrm{SES}\ i,k}$). Then, Var($\Delta\beta_{i,k}$) is calculated as the sum of the elements of $\boldsymbol{C}_{i,k}$. To introduce noise into the predictor values in the regression model, a random number derived from a normal distribution with a mean of zero and a standard deviation of $\sqrt{\mathrm{Var}\left(\Delta\beta_{i,k}\right)}$, was added to the $\Delta\beta_{i,k}$ estimate. This process was repeated 5000 times to obtain an empirical distribution of the effect of $\Delta\beta_{i,k}$, which now includes the uncertainty of the change of betas between the seasons. Medians and 95% confidence intervals of these parameter estimates derived from these empirical distributions are presented in the Supporting information.

Results

Resource selection functions (RSFs) and habitat usage

There was a trend toward smaller home range areas in spring/early summer (SES; May–June: 498 ± 143 km^2) compared to late summer/autumn (LSA; July: 683 ± 231 km^2), but the difference was only marginally non-significant (Wilcoxon signed-rank test: $V=64$, $p=0.052$). The average seasonal difference in home range (ΔHR) was 184 ± 289 km^2, with considerable individual variation. During the early growing season, reindeer primarily used lichen pastures (SES: 58 ± 3%), but this declined significantly by 11% (LSA: 47 ± 6%; $p=0.002$) in late summer/autumn. This shift was accompanied by increased use of mires and bogs (MB; SES: 20 ± 4%; LSA: 27 ± 8%; $p=0.002$), dwarf shrub and grass pasture (DSGP; SES: 17 ± 2%; LSA: 20 ± 4%) and bare fell/mountain areas (BFM; SES: 2 ± 1%; LSA: 4 ± 3%). Individual variation in vegetation type usage was observed both within and between seasons.

Reindeer consistently selected higher elevations across both seasons (Fig. 2), indicating no seasonal shift in elevation preference (+ → +; Supporting information). However, the proportion of individuals showing significant selection for elevation increased by 8% from SES to LSA (Supporting information).

Greener areas, as indicated by NDVI, were preferred in both seasons (Fig. 2), with 33% of individuals shifting from random selection in SES to preference in LSA (RS → +). Rugged terrain was avoided by 67% of individuals during SES, but this declined to 17% in LSA (Fig. 2, Supporting information). This shift (– → RS) in 50% of individuals reflects reduced avoidance rather than an increased preference for rugged terrain.

Reindeer preferentially selected mires and bogs (MB) over the reference class, lichen pasture (LP), while dwarf shrub and grass pastures (DSGP) and bare fell/mountain areas (BFM) were neither preferred nor avoided (Fig. 2). Selection for MB increased in LSA, with 42% of individuals shifting from random selection to preference across the seasons (RS → +; Supporting information). Pasture selection remained random (RS → RS) with respect to DSGP for 92% of individuals, while BFM selection shifts varied: 25% of individuals shifted from random selection in SES to preference in LSA (RS → +), and 8% shifted from avoidance to random selection (– → RS). Overall, all the reindeer altered their selection for at least one habitat variable (Supporting information), demonstrating individual-level variability in resource selection and seasonal shifts, patterns consistent with the habitat selection generalist (HS$_\mathrm{G}$) predictions (Table 2).

Isotopic niches and trajectories

Mean δ^{15}N and δ^{13}C values were significantly enriched from SES to LSA (Wilcoxon signed-rank test: δ^{15}N, $V=6$, $p=0.007$; δ^{13}C, $V=14$, $p=0.052$), indicating a shift towards increased consumption of δ^{15}N-enriched plant species (Supporting information) during LSA. Individuals exhibited substantial variation in trajectory length (X_i; range: 0.24–1.18) and direction (θ_i; range: 0.29–5.23). However, the observed trajectory angles (Fig. 3a; inset) showed no significant directional trends ($U=166.21 < U_{0.05}=169.09$), indicating a random distribution of dietary shifts between the seasons. The isotopic ellipse for SES ($\mathrm{SEA_C}=0.22$, $\mathrm{SEA_B}=0.20$, 95% CI: 0.09–0.48) was nested within the LSA ellipse (Fig. 3a) and was significantly smaller ($\mathrm{SEA_C}=0.55$, $\mathrm{SEA_B}=0.48$, 95% CI: 0.22–1.14, $\mathrm{PP_{SES<LSA}}=0.017$; Fig. 3b). The overlap between the seasons was limited to 31.7%. These dietary shifts, reflected in the trajectory angles and isotopic niches, align with predictions that reindeer exhibit a diet selection generalist (DS$_\mathrm{G}$) response (Table 2, Supporting information).

Linking seasonal shifts in habitat and diet selection

As the reindeer in the current study followed a generalist habitat–diet foraging strategy (Table 1–2), the analysis proceeded to evaluate potential linkages between seasonal shifts in habitat and diet selection. Multiple models were tested using various combinations of dietary response variables and habitat selection explanatory variables (Supporting information), but only the best-fitting models for each diet metric are presented in Table 3. Of all these models, only one habitat metric, the seasonal shift in the selection coefficients for terrain ruggedness ($\Delta\beta_{\mathrm{rug}}$), had a significant effect on a diet shift metric: $\sin\theta_i$ was negatively affected by terrain ruggedness ($\beta= -1.7085 \pm 0.4957$, $p=0.0063$). This effect was further supported by the sensitivity analysis (Table 2). Although none of the

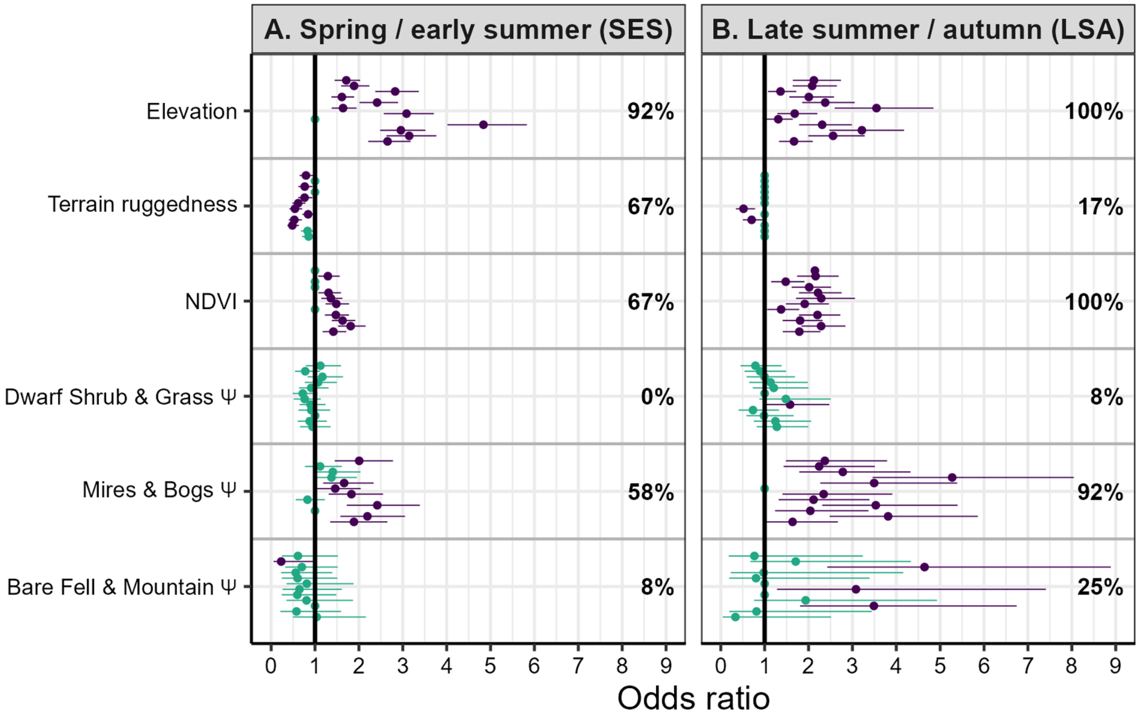

Figure 2. Comparison between the seasons (A) spring/early summer (SES) and (B) late summer/autumn (LSA) of the odds ratios of habitat and pasture selection derived from the resource selection models. The habitat variables include elevation (elev), terrain ruggedness (rug), and the Normalised difference vegetation index (NDVI). Pasture class variables are compared to the reference category, lichen pasture (LP) indicated by **Ψ**: dwarf shrub and grass pasture (DSGP), mires and bogs (MB) and bare fell and mountain pasture (BFM). Each point represents the odds ratio of the estimate for each reindeer, and the whisker indicates the 95% confidence intervals. Points and whiskers in purple are statistically significant; those in turquoise are not. The black line at one (1) indicates random selection (RS), with values less than one (< 1) indicating avoidance (–) and values greater than one (> 1) indicating preference (+). The '%' symbol denotes the percentage of females/season that preferred or avoided each resource.

habitat selection variables had significant effects on X_i and $\cos\theta_i$, the best-fitting models included the seasonal change in the proportion of pasture use for X_i and the habitat selection coefficient for NDVI for $\cos\theta_i$ (Table 3).

It is important to clarify the meanings of variables $\Delta\beta_{rug}$ and $\sin\theta_i$ in the current dataset to understand this significant relationship. In spring/early summer (SES), 67% of individual reindeer avoided rugged terrain, whereas, in late summer/autumn (LSA), 50% of these individuals shifted toward random choice with respect to terrain ruggedness, i.e neither avoidance nor preference. A higher $\Delta\beta_{rug}$ value reflects a greater reduction in rugged terrain avoidance. Dietary shifts, as measured by $\sin\theta_i$, are more complex. The $\sin\theta_i$ metric represents the ratio of the seasonal difference in $\delta^{15}N$ ($\Delta^{15}N$) to Xi ($\Delta^{15}N/X_i$; Supporting information), with all values falling between 0 and 1, reflecting two distinct scenarios:

1) $\Delta^{15}N < X_i$ ($\sin\theta_i < 1$): In this case, the dietary shift is driven by a significant difference in $\delta^{15}N$ between SES and LSA, accompanied by a substantial change in $\delta^{13}C$, such that the isotopic trajectory distance (X_i) exceeds $\Delta^{15}N$. Approximately 67% of the reindeer exhibit this shift, transitioning their diets from SES to LSA by feeding on plants more enriched in both $\delta^{15}N$ and $\delta^{13}C$. These dietary changes likely involve a shift from lichen, deciduous trees, shrubs and dwarf shrubs to sedges, grasses, horsetails and mushrooms (Supporting information).
2) $\Delta^{15}N \approx X_i$ ($\sin\theta_i \approx 1$): Here, the dietary shift is driven by a significant difference in $\delta^{15}N$ between SES and LSA, which is nearly equal to the isotopic trajectory distance (X_i), with minimal changes in $\delta^{13}C$. This pattern is observed in 33% of the reindeer, which forage in LSA on plants more enriched in $\delta^{15}N$ but with similar $\delta^{13}C$ values to those consumed in SES. These isotopic shifts suggest three possible dietary transitions: 1) lichens to horsetails; 2) evergreen dwarf shrubs to grasses; and 3) grasses to sedges (Supporting information).

Discussion

This is the first study, to our knowledge, to integrate stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) with GPS tracking data to examine seasonal habitat and diet selection in a generalist herbivore. The results reveal clear seasonal shifts in both habitat and diet selection between spring/early summer (SES) and late summer/autumn (LSA; Table 2), supporting the hypothesis that Kaldoaivi reindeer are habitat–diet generalists (Table 1). These shifts reflect the plasticity of reindeer foraging strategies and

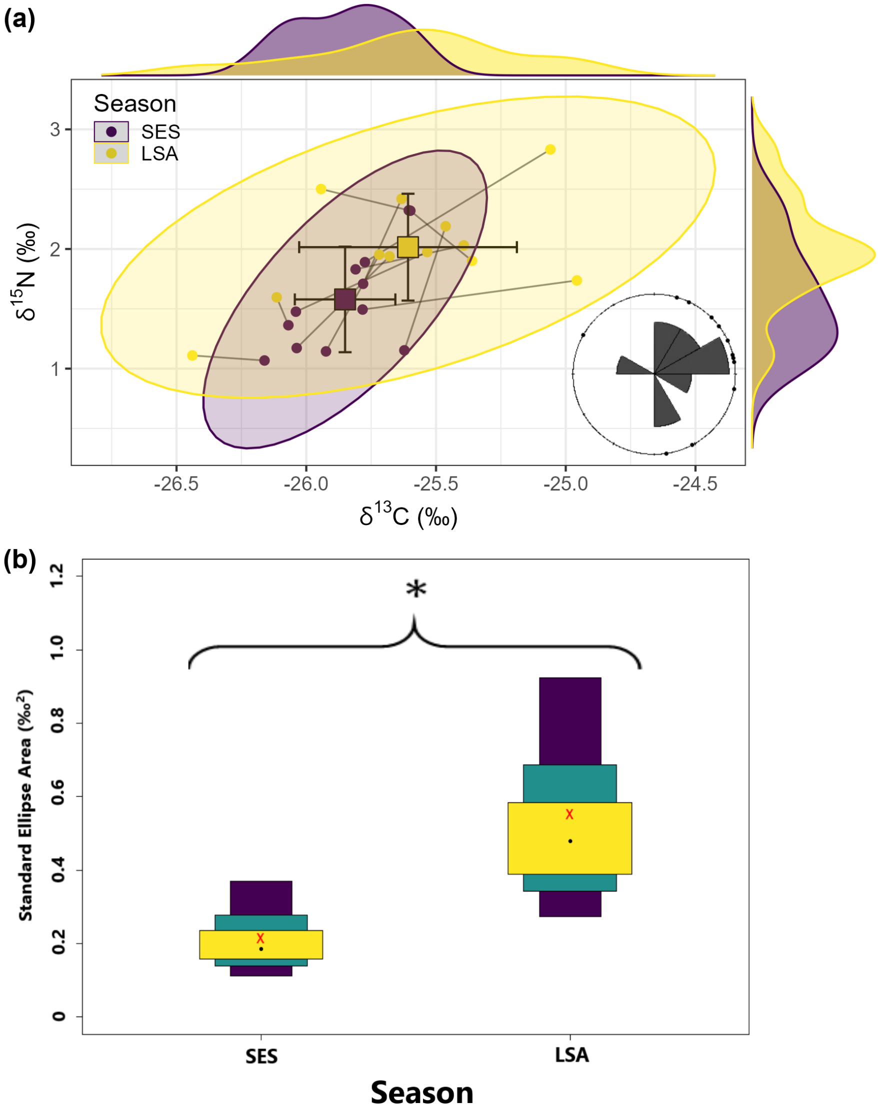

Figure 3. (a) Bivariate plots of hair $\delta^{13}C$ and $\delta^{15}N$, with individual reindeer niche trajectories represented by vectors connecting hair section B (i.e spring/early summer growth, SES, purple) and hair section A (i.e late summer/autumn growth, LSA, yellow) isotope values for each reindeer ($n = 12$). Squares indicate mean values, and the error bars represent standard deviations. Density plots along the x- and the y-axis show the distribution of the $\delta^{13}C$ and $\delta^{15}N$ values, respectively. The inset displays the observed circular distribution of individual reindeer niche trajectory angles. Isotopic niches are represented by the 95% SIBER standard ellipse areas (SEA) corrected for small sample sizes (SEA_C) of reindeer hair isotope values for spring (blue) and summer (red). (b) Boxplot of the Bayesian standard ellipse areas (SEA_B) from 10^4 replicates for each season, modelled in SIBER. Black dots represent the mode, red crosses indicate the mean, and the boxes show the 50, 75, and 95% credible intervals. Significance was determined by comparing the proportion of posterior ellipses that differed between the seasons (PP). Differences in SEA_B were considered significant if $PP \geq 0.95$ and are denoted as follows: $p < 0.05$ (*).

provide a unifying temporal scale for interpreting diet–habitat relationships. Reindeer exhibited reduced avoidance of rugged terrain ($\Delta\beta_{rug}$) from SES to LSA, a shift linked to dietary changes represented by sin θ_i. The isotopic diet shift reflects a transition from a diet dominated by plants depleted in $\delta^{15}N$ or both $\delta^{15}N$ and $\delta^{13}C$ (e.g. lichens, evergreen dwarf shrubs, deciduous trees, shrubs and dwarf shrubs; Supporting information) to species enriched in $\delta^{15}N$ or both $\delta^{15}N$ and $\delta^{13}C$ (e.g. sedges, grasses, horsetails and mushrooms; Supporting information). Dietary shifts between summer and autumn are common across *Rangifer* populations (Mårell and Edenius 2006, Vors and Boyce 2009, Drucker et al. 2010, Åhman and White 2018). However, habitat selection patterns can vary considerably depending on regional landscape characteristics. In Kaldoaivi, this variation is evident in the avoidance of rugged terrain during SES and random selection in LSA, contrasting with patterns observed in other regions (Nellemann and Thomsen 1994, Nellemann and Fry 1995, Mårell and Edenius 2006, Hansen et al. 2009, Joly 2011).

Rugged terrain is associated with diverse vegetation, variable snow conditions, and heterogeneous snowmelt regimes, all of which enhance foraging opportunities. However,

Table 3. Parameter estimates (β ± SE) from the best-fit linear regression models predicting diet shifts based on shifts in habitat selection. Predictors with statistically significant parameter estimates are highlighted in grey and bold black text. The response variables are diet shift metrics: Xi or the sine or cosine of θi, while the explanatory variables are habitat shift metrics: differences in the seasonal pasture use (ΔPropPast) or selection coefficients (Δβi,k) for elevation (elev), terrain ruggedness (rug), NDVI and pasture types (bare fell and mountain pasture [BFM]; dwarf shrub and grass pasture [DSGP]; mires and bogs [MB]; relative to lichen pasture [LP]). Statistical significance is denoted as follows: $p < .001$ (***); $p < .01$ (**); $p < .05$ (*). A sensitivity analysis was conducted to account for uncertainty arising from the RSF regression coefficients used to derive the Δβ values included as predictors in the linear models. For the RSF β uncertainty test, each regression model was refitted using predictor (Δβi,k) values randomly drawn from individual-specific distributions, reflecting the uncertainty (median, 95% confidence intervals [CI]) associated with each reindeer's Δβi,k estimate. The outputs of all linear regression models are presented in thye Supporting information.

		RSF model							RSF β Uncertainty test		
Model Formula	Model no.	Coefficient	Estimate	SE	*t* value	Pr(>|t|)	Multiple R^2	Adjusted R^2	Median (CI: 50%)	CI: 2.5%	**CI: 95.7%**
$X_i \sim \Delta Prop_{BFM}$	t7	Intercept	0.745	0.094	7.913	0.00001***	0.201	0.121	NA	NA	NA
		$\Delta Prop_{BFM}$	−4.664	2.941	−1.586	0.144					
$\sin\theta_i \sim \Delta\beta_{rug}$	s2	Intercept	0.901	0.148	6.106	0.00012***	0.543	0.497	−1.708	−2.036	−0.689
		$\Delta\beta_{rug}$	−1.709	0.496	−3.447	0.0063**					
$\cos\theta_i \sim \Delta\beta_{NDVI}$	c3	Intercept	0.830	0.404	2.055	0.067	0.217	0.139	−1.477	−2.020	−0.194
		$\Delta\beta_{NDVI}$	−1.477	0.888	−1.664	0.127					

Kaldoaivi's low mean ruggedness index (mean = 8.83 ± 9.14, min = 0.0, max = 207.40) suggests a predominantly flat landscape, particularly on the Riley et al. (1999) ruggedness scale, where values between 0 and 80 represent 'relatively level surfaces'. In landscapes where movement into rugged terrain or high elevations is limited, *Rangifer* species such as woodland caribou *R. t. caribou* and Finnish forest reindeer *R. t. fennicus*, select a mosaic of habitats that optimise foraging while minimising predation risk (Rettie and Messier 2000, Kojola et al. 2004). In contrast, Svalbard reindeer *R. t. platyrhynchus*, which inhabit rugged landscapes with low predation pressure, prioritise foraging opportunities over terrain ruggedness (Garfelt-Paulsen et al. 2021). Kaldoaivi reindeer also experience low predation pressure relative to other Finnish herding districts (Paliskuntain Yhdistys 2020). Given this combination of low predation pressure and a relatively flat landscape, the lack of preference for rugged terrain by Kaldoaivi reindeer likely reflects a strategy to maximise foraging efficiency, consistent with predictions from optimal foraging theory (Ferguson and Elkie 2004, Mårell and Edenius 2006, Ehlers et al. 2021, Romtveit et al. 2021).

Unlike rugged terrain, higher elevations and greener areas (i.e areas with high NDVI) were consistently selected throughout the snow-free season. Despite the limited altitudinal range (mean = 259 ± 68 m a.s.l., min = 10, max = 446 m a.s.l.) in Kaldoaivi, the findings are consistent with other studies. For example, in the mountainous regions of Sweden (332–2015 m a.s.l.), reindeer move to high-elevation, rugged ridge heaths in spring, where thinner snow cover allows earlier access to vegetation (Mårell et al. 2006, Skarin et al. 2008, Ophof et al. 2013). As the snow retreats and calves become more mobile (Laptander et al. 2024), reindeer track the sequential emergence of nutritious green vegetation, descending from lichen pastures to flatter, wetter areas (Skogland 1984, Klein 1990, Danell et al. 1994, Skarin et al. 2008, Åhman and White 2018, Laptander et al. 2024). The aquatic and terrestrial vegetation in these habitats provide essential protein and minerals, replenishing nutrient deficits from a lichen-dominated winter diet and supporting the demands of calving and lactation (McEwan and Whitehead 1970, Nieminen 1986, Staaland and Sæbø 1993, Skarin et al. 2008).

Peak protein and nutrient concentrations in vegetation occur between mid-June and early July, declining by late August (Klein 1990, Staaland and Sæbø 1993, Mårell et al. 2006, Iversen et al. 2014, Berthelot et al. 2025). Early in the season, forbs, deciduous shrubs and trees provide high concentrations of proteins, carbohydrates, and nutrients, while grasses initially exceed sedges in protein content; this reverses later in the season (Chapin III et al. 1975, Trudell and White 1981, Klein 1990, Mårell and Edenius 2002, Berthelot et al. 2025). This early-season availability of protein-rich vegetation is reflected in the depleted $\delta^{13}C$ and $\delta^{15}N$ values observed in SES, which indicate consumption of deciduous trees, shrubs, and dwarf shrubs, alongside winter forage plants such as lichens and evergreen dwarf shrubs – all of which are isotopically depleted compared to other plant functional groups (Supporting information).

As green vegetation becomes widespread and insect harassment increases, reindeer expand their movements and home ranges (Mårell and Edenius 2006, Skarin et al. 2008, Johnson et al. 2021). To balance nutrient intake with the energy costs of heat stress and insect harassment avoidance, blood loss and antler growth, reindeer continue to select protein- and nutrient-rich plants (Nieminen and Heiskari 1989, Klein 1990, Johnson et al. 2021). During this period, key forage and nutritional resources are found in habitats dominated by forbs, grasses, sedges, deciduous trees and shrubs (Mårell et al. 2002, Pääkkö et al. 2019), which is consistent with the vegetation classes selected in the current study. Many of these plant groups, particularly sedges, grasses, horsetails and some forbs, are enriched in $\delta^{13}C$ and $\delta^{15}N$ (Supporting information), and their increased consumption likely accounts for the corresponding enrichment observed in the hair isotope values during LSA. However, as autumn approaches, declining nitrogen levels and shifting nutrient availability alter reindeer foraging strategies, with an increasing focus on energy storage rather than protein maximisation.

By late summer, although plant quality declines, biomass remains high. Reindeer prioritise fat accumulation by consuming energy-dense forage such as mushrooms (Nieminen and Heiskari 1989, Klein 1990). When mushrooms are scarce, as in Kaldoaivi in autumn 2019 (Kumpula et al. 2020, pers. obs. 2019), reindeer compensate by consuming large quantities of grasses, sedges, and other available plants before increasing their intake of lichens (Nieminen and Heiskari 1989, Mårell and Edenius 2006, Inga 2009, Bezard et al. 2015). This shift to a broader dietary mix, including both isotopically enriched and depleted plant species, likely contributed to the significantly expanded isotopic niche observed toward the end of the growing season.

Beyond these seasonal patterns, interindividual differences in isotopic trajectories likely arise from several interacting mechanisms. Variation in late-winter, spring and summer forage use, including differences in the proportions of plant species consumed and the spatial and temporal variation in plant $\delta^{13}C$ and $\delta^{15}N$ values, combined with the cumulative nature of isotope incorporation to produce distinct individual isotopic values (Nieminen and Heiskari 1989, Bearhop et al. 2004, Yeakel et al. 2016). Physiological differences in gut microbiome composition, digestive efficiency and nutrient assimilation, may further modify individual isotope values by altering diet-to-tissue routing (Hobson 2023, Kamenova et al. 2025). Unequal access to vegetation patches of differing quality and to locally variable forage plant availability, and ephemeral resource pulses (Dwinnell et al. 2024) such as autumn mushroom flushes, adds further divergence among individuals.

Dietary and physiological differences are reinforced by behavioural variation, as individuals differ in foraging experience, age-specific movement capacity and reproductive status, and in the spatial and attribute memory that governs route reuse and the timing of resource encounters (Avgar et al. 2015, Jesmer et al. 2025, Verzuh et al. 2025). Competition also modifies resource access and amplifies within and among individual variability in diet composition (Bolnick et al. 2010). As all collared individuals were adult females, none of the observed isotopic variation reflects sex-based differences in foraging ecology. Collectively, these ecological, physiological and behavioural mechanisms generate the broad range of isotopic trajectory magnitudes observed between SES and LSA.

Seasonal changes in physiological demands and nutritional requirements, coupled with changes in forage quality and availability, drive shifts in diet, movement and habitat selection. These seasonal behavioural shifts are reflected in expanded home ranges (Skarin et al. 2008) and the broadening isotopic niche observed in this study. These findings underscore how reindeer adopt flexible foraging strategies to navigate seasonal nutritional trade-offs in heterogeneous environments, where the interplay of bottom-up and top-down controls is key to the success of ungulates in Arctic and boreal ecosystems (Clark-Wolf et al. 2025).

Conclusion

This study highlights the value of integrating GPS-based movement data, spatiotemporal habitat covariates, and stable isotope analysis to unravel the interplay between habitat and diet selection. By combining spatial and isotopic data, this approach overcomes the limitations of single-method studies, offering a more nuanced understanding of seasonal foraging dynamics. Thresholds introduced within this framework detect seasonal shifts in habitat and diet selection and classify foraging strategies along a specialist–generalist continuum. Despite a small sample size, these thresholds revealed that Kaldoaivi reindeer are generalists in both habitat and diet selection, using flexible foraging strategies to meet changing seasonal demands while balancing nutritional needs with insect harassment and predation in a variable environment. Although all individuals in the study exhibited variation in both habitat and diet selection in and between spring and autumn, this flexibility suggests that reindeer possess the foraging plasticity needed to respond to ongoing environmental changes, at least within the bounds of the current seasonal window.

The integrative framework improves our understanding of reindeer ecology and provides a scalable tool for investigating seasonal foraging strategies in other generalist herbivores. It also has broader relevance for assessing ecological risk. In some species, such as the least chipmunk *Neotamias minimus*, populations differ in their position along the specialist–generalist continuum, with important implications for conservation. For example, habitat loss is driving the decline of the southernmost subspecies *N. m. atristriatus*, which, unlike the other more generalist subspecies, has been identified as a specialist (McKibben and Frey 2025). This highlights the importance of empirically evaluating ecological strategies across subpopulations rather than relying on species-level assumptions when assessing vulnerability to habitat change.

Understanding individual variability in foraging strategies is critical for predicting population-level responses to climate-driven habitat changes and informing adaptive management. Future work integrating ecological, physiological, and socio-environmental data will be key to fully capturing the complexity of ungulate responses to environmental change. These findings lay the foundation for future research on foraging plasticity and ecological vulnerability in the face of accelerating climate change and habitat fragmentation. Integrating spatial and dietary data can also support adaptive management strategies for reindeer herding communities and inform land-use decisions in Arctic and boreal regions. Broader sample sizes and multi-regional comparisons will be essential for a comprehensive understanding of how dynamic environmental conditions influence habitat and diet selection and to inform effective conservation and management strategies.

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Author contributions

Tamara A. Hiltunen: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Sami M. Kivelä**: Formal analysis (supporting); Methodology (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Jouko Kumpula**: Conceptualization (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jouni O. Aspi**: Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Supervision (equal); Writing – review and editing (supporting). **Jeffrey M. Welker**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (equal); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5x69p8djm (Hiltunen et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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