

Integrating movement behaviours for intra-specific conservation: The caribou case

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ABSTRACT

Conserving diversity below the species level is vital to maintaining species' adaptive potential. However, defining intra-specific units for conservation is complex due to the often-continuous nature of differentiation, and thus multiple lines of evidence are needed to adequately capture adaptive differences. Caribou (*Rangifer tarandus caribou*) exemplify this challenge, exhibiting diverse behavioural, genetic, and morphological variation throughout their range, with several populations facing extirpation. We used a long-term telemetry dataset of 302 caribou across the species' range in western Canada to assess individual variation in movement behaviours. This included behaviours hypothesized to be of adaptive significance, such as migration, home range size and shape, and inferred predator avoidance tactics. Gaussian finite mixture models were then used to identify intra-specific behavioural clusters which may be evolutionarily significant, followed by Random Forest models to discern behaviours driving differentiation between clusters. We identified six distinct clusters based on individual variation in behaviour. Differentiation between clusters was significantly influenced by selection for canopy cover (%) at calving events, home range size and shape, migratory behaviour, and geographic location. Since behavioural variation arises from genetic, environmental, and social factors, our results highlight the value of incorporating trait variation into the assessment of evolutionarily significant units for conservation. We advocate for the consideration of behavioural variation, as it offers valuable insights into adaptive differences. This approach holds promise for informing conservation efforts, not only for caribou, but other terrestrial species at risk given the importance of maintaining genetic and phenotypic diversity.

1. Introduction

Genetic and phenotypic variation are important aspects of biodiversity and essential to a species' legacy, ensuring its adaptive potential is protected (Dimmick et al., 1999). Intra-specific genetic diversity and phenotypic variation, such as behaviour, provide the foundation for evolutionary processes, allowing populations to respond to

environmental changes through natural selection (Clutton-Brock, 1988; Coates et al., 2018). Behaviour may influence survival, reproductive success, and demographic connectivity of populations (Hawkes, 2009), is often hereditary (Anthony and Blumstein, 2000; Bubac et al., 2020; Whiten, 2017), and may be socially transmitted (Coussi-Korbel and Fragaszy, 1995; Pinter-Wollman et al., 2008).

Since gregarious species often exist as multiple groups or

Abbreviations: ESU, Evolutionary Significant Unit; KDE, Kernel Density Estimate; RF, Random Forest; DU, Designatable Unit; MCP, Minimum Convex Polygon; MDA, Mean Decrease Accuracy; m, meters; DEM, Digital Elevation Model; OOB, Out of Bag (error); m.a.s.l., meters above sea level; IO, Index of Overlap.

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subpopulations across a landscape with some level of genetic and/or phenotypic differentiation, a singular approach to species conservation is often not appropriate (Allen and Singh, 2016; Arendt, 2015). It is therefore critical to understand where to define boundaries between populations for the effective allocation of conservation resources. Yet this proves challenging due to the continuous nature of differentiation among populations and the complexity of identifying biologically relevant intra-specific variation (Butlin, 2010; Coates et al., 2018; Moritz, 1994).

Many regulatory frameworks employed by governing bodies (such as the Species at Risk Act; SARA, and the US Endangered Species Act; ESA) recognize the importance of identifying distinct populations as a fundamental objective for conservation and management, allowing for protection of biologically distinct entities below the species level (Findlay et al., 2009; Weckworth et al., 2018). The concept of Evolutionarily Significant Units (ESUs) provides one basis for prioritizing and defining intra-specific units for conservation purposes (Moritz, 1994; Ryder, 1986a, 1986b). Various definitions in the literature concur that individuals within a given ESU should display concordant divergence for neutral genetic variation, adaptive genetic variation, and phenotypic traits (Davis et al., 2005; Moritz, 1994). However, Hoelzel (2023) proposed refining the ESU concept through first identifying conservation units broadly, and then assessing divergence quantitatively to recognize distinct evolutionary trajectories. This should include phenotypic divergence, as it may be useful in quantifying biodiversity and predicting future diversification (Phillimore et al., 2008).

Intra-specific units may be delineated using multiple lines of evidence and methodologies, including evaluation of population structure using genetic information, adaptive differentiation, ecological and behavioural differentiation. This is often achieved through clustering or ordination techniques to evaluate genetic variation (Bernard et al., 2009; Coates et al., 2018; Funk et al., 2012; Turbek et al., 2023).

Measures of genetic diversity provide valuable insight into the evolutionary history and potential of populations (Coates et al., 2018). However, genetic clustering methods have the potential to under-represent phenotypes of adaptive significance (de Guia and Saitoh, 2007). Furthermore, local adaptation can take place despite the presence of high gene flow (Saint-Laurent et al., 2003), with species exhibiting phenotypic diversity in the absence of genetic differentiation (Baack and Rieseberg, 2007; Hedrick, 2013; Sadanandan et al., 2020). For example, Ben Cohen and Dor (2018) demonstrated patterns of phenotypic divergence in morphological, colouration, and behavioural traits across house sparrow (*Passer domesticus*) ranges despite low genetic differentiation. Similarly, Bal et al. (2021) found comparable levels of genetic diversity and neutral genetic differentiation among populations of three-spined sticklebacks (*Gasterites aculeatus*) between well connected but environmentally heterogeneous habitats, observing distinct signatures of morphological and adaptive divergence.

In Canada, Caribou (*Rangifer tarandus*) provide a unique example of the ongoing challenge of identifying intra-specific conservation units. Rapidly changing climatic conditions and anthropogenic disturbances have led to dramatic declines of caribou across Canada (Festa-Bianchet et al., 2011; Hervieux et al., 2013; Weckworth et al., 2018). Caribou are distributed across much of Canada's northern regions and are adapted to a diverse range of habitat types, displaying a tremendous amount of genetic, morphological (e.g. pelage coloration or body size), and behavioural (e.g. migratory tendency or habitat preferences) variation across their range (Festa-Bianchet et al., 2011; Weckworth et al., 2018). Canada is home to three sub-species of caribou currently recognized federally based on their distinctiveness in genetics, morphology, or ecology: peary- (*R.t. pearyi*), barren-ground- (*R.t. groenlandicus*), and woodland caribou- (*R.t. caribou*) (Bergerud, 2000, 1996, 1988; Hebblewhite et al., 2010; Hummel and Ray, 2008; SARA, 2014). Woodland caribou, the focus of this work, are then further split into various intra-

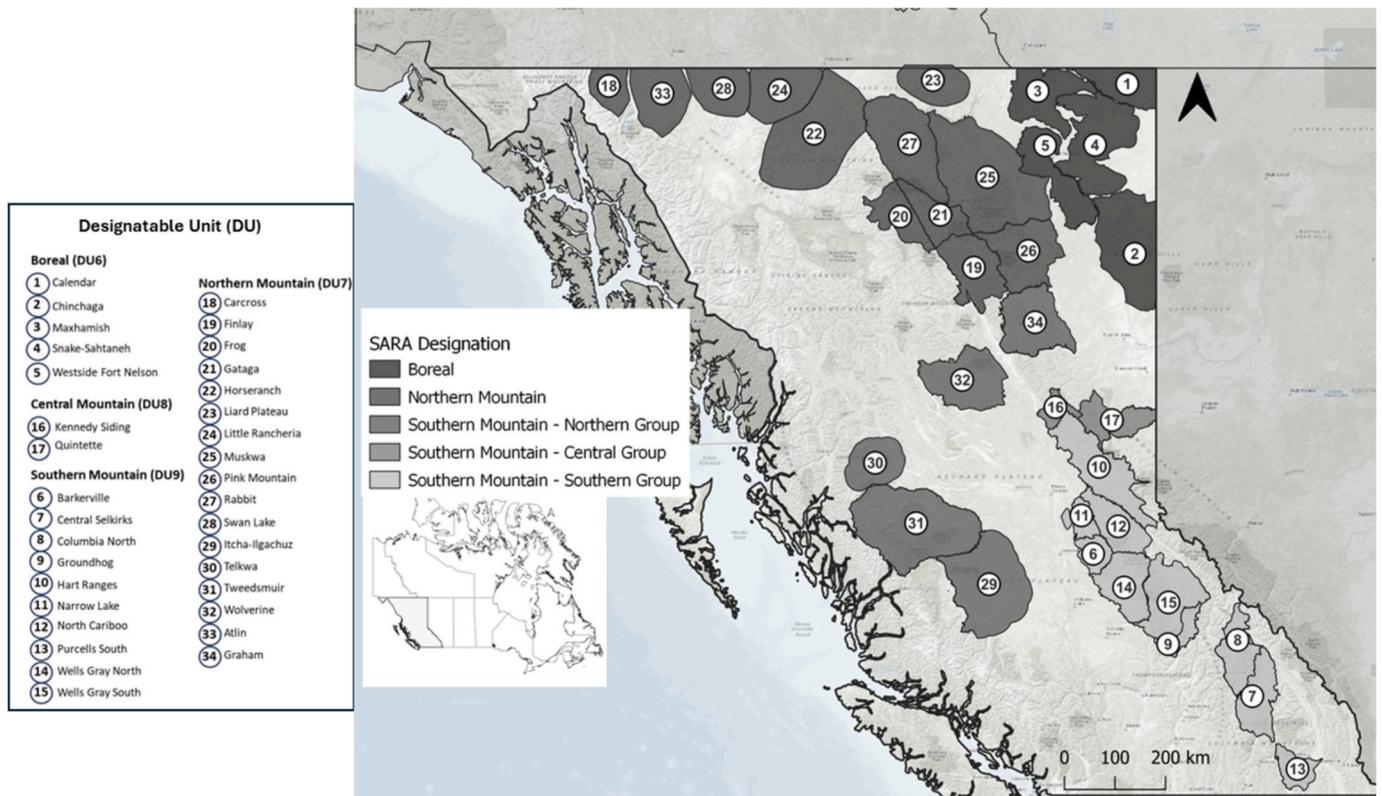


Fig. 1. Study area, with all population boundaries (see Ministry of Environment and Climate Change Strategy, Government of British Columbia, 2021). Populations are grouped by the population designation in the Species at Risk Act (SARA, 2014, 2002), highlighted by range and gray-scale on the map. The circled numbers show caribou populations in Designatable Units (DU) as evaluated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2011).

specific units for conservation at the federal level (Fig. 1, SARA, 2014, see also Table A 1). Behavioural variability has previously been observed at both population and individual levels across the sub-species range. For example, variation in movement behaviour, such as seasonal migration, home range use patterns (Bergerud et al., 1990; Bergerud, 2000; Pond et al., 2016; Blagdon and Johnson, 2021; Cavedon et al., 2022b; Theoret et al., 2022), and hypothesized predator avoidance tactics (Bergerud et al., 1990; Bergerud and Page, 1987; Cameron et al., 2020; Nobert et al., 2016) have been demonstrated between individuals and populations.

To account for this variation in conservation, 12 Designatable Units (DUs), which are defined similarly to ESUs, were identified for caribou by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC, 2011). DUs were delineated based on genetic, phylogenetic, or behavioural differentiation, ecology, and geographical distribution, with designation based on significant discreteness in at least one line of evidence (COSEWIC, 2018). However, identified DUs do not fully align with the intra-specific units defined by SARA for caribou within Canada, which might negatively influence conservation planning (see: Hummel and Ray, 2008; McDevitt et al., 2009; Pond et al., 2016; Weckworth et al., 2018; Yannic et al., 2016). While DU designation employs multiple lines of evidence, there is a focus on the genetic data (Weckworth et al., 2018). Alternatively, ecotypes, which are broadly defined on hypothesized differences in life history strategies and behaviours (Morrison, 2012; Pond et al., 2016), are another term commonly used to delineate caribou intra-specific units provincially and within the literature, further differ from both DUs and SARA designations.

The woodland caribou sub-species are habitat specialists, typically maintaining low population densities in large tracts of coniferous old-growth forests or boreal peatland where diets rely on terrestrial or arboreal lichens during specific periods of the year (Hebblewhite, 2017; Thomas et al., 1996). In British Columbia, woodland caribou are often classified into three ecotypes: northern and mountain, mainly including migratory individuals, and boreal mainly including sedentary individuals. Four DUs are also recognized: Boreal, Northern Mountain, Central Mountain, and Southern Mountain (COSEWIC, 2011; Hummel and Ray, 2008; Pond et al., 2016). Females within the sedentary ecotype are thought to isolate themselves from other parturient females selecting for areas with greater canopy cover to calve (Barten et al., 2001; Bergerud and Page, 1987), whereas migratory females are thought to move away from areas with high densities of other prey species, selecting for areas of high elevations during the calving season (Gustine et al., 2006; Gustine and Parker, 2008; Nobert et al., 2016; Wittmer et al., 2006). Differences in movement patterns such as differing proportions of migratory individuals within herds or populations, including altitudinal migration (Blagdon and Johnson, 2021; Cavedon et al., 2022b; Theoret et al., 2022), variation in size and shape of home ranges (Pond et al., 2016; Wilson et al., 2019), and differences in foraging strategies (Apps et al., 2001b; Cavedon et al., 2022a; Terry et al., 2000) have previously been observed between DUs and ecotypes of woodland caribou. In addition to behavioural variation, genetic isolation (Ball et al., 2010; Cavedon et al., 2022a; Michalak, 2023; Yannic et al., 2016), phylogenetic hybrid zones (McDevitt et al., 2009), and geographical distribution further contribute to uncertainty in defining intra-specific units.

Here we capitalize on a multi-year, broad-scale telemetry dataset to investigate variation in individual movement behaviours of potential adaptive significance for female caribou in western Canada. Telemetry data in which animals are monitored for at least one year allow for the measurement of various metrics of movement (such as seasonal migration; Theoret et al., 2022), calving (date and strategy; Cameron et al., 2020; Nobert et al., 2016; Pond et al., 2016), and habitat space use (elevation use, home range size, and home range shape; Pond et al., 2016; Servheen and Lyon, 1989; Terry et al., 1996; Wilson et al., 2019). Since behavioural differences have been observed or assumed to define ecotypes and DUs, we hypothesized that caribou could be grouped based

on variation in individual behaviour. Our goal was to identify which behaviours may be discrete between potential caribou intra-specific units to inform the designation of conservation units. Focusing on individual variation in measured behaviours, rather than comparisons between pre-defined populations (or sub-population units), offers a novel perspective to aid in the delineation of potential evolutionary and conservation units of terrestrial species. We predicted that differences in migratory and calving strategies as well as differences in home range size and shape would significantly contribute to discreteness between potential intra-specific units of woodland caribou. Furthermore, due to differences in the habitats that individuals encounter throughout the study area, the location an individual occupied was predicted to influence behavioural differentiation.

2. Methods

2.1. Study area

Our study area is approximately 962,416 km², ranging across the Rocky Mountains and boreal forest of Western Canada (mainly British Columbia) (Fig. 1). This includes both protected parklands as well as private and multi-use public lands. The climate is characterized by long winters and short summers, with precipitation increasing from east to west. Habitat types include montane, subalpine, and alpine ecoregions (Holland and Coen, 1983; Mah et al., 1969). The topography includes flat valley bottoms surrounded by steep slopes of the Rocky Mountains (400–3937 m above sea level; m.a.s.l.). Roads, seismic exploration lines, railways, and logging areas are common throughout the study area, leading to habitat fragmentation and forest loss within recent years (Oduro Appiah et al., 2021).

2.2. Data collection and screening

Female caribou were captured, via helicopter net-gunning or darting, and GPS telemetry collars were deployed (either Lotek or Vectronics) by trained personnel, British Columbia wildlife officials, and other government and parks agency partners between 2014 and 2023, following government standardized animal care permits, and handling procedures. The focus was on the collaring of female caribou, as provincial government protocols consider females as a first monitoring priority for conservation (McDevitt et al., 2009; Theoret et al., 2022). Females are also ideal for defining seasonal movements, as individuals show high fidelity to areas used during a fixed calving period (Bergerud et al., 2008). To maximize battery life, collar fix rates varied from hourly (in seasons needing information relevant to conservation, such as calving) to every 7 days and therefore remained on animals for variable periods of time (minimum of 2 months and maximum of 6 years). All locations within the first 24 h after capture were excluded (Jung et al., 2019) and erroneous locations were removed, through initial visual inspection of the data and removing obvious errors (i.e., fixes that exceeded the possible range or movement of the animal), following Cagnacci et al. (2016). Filtering was then done to ensure that each individual met the minimum data requirements (see below) for behavioural analyses. This resulted in a dataset of 456,010 locations between 2014 and 2023 from 302 individuals across 34 predefined subpopulations (Fig. 1; see The British Columbia Caribou Recovery Program, 2023). Here, subpopulations refer to a group of individuals occupying a single range which may be a subset of a larger population (Environment Canada, 2014). Data relating to elevation in meters above sea level (m.a.s.l.) was at a resolution of 30 m (m) and obtained from the Canadian Digital Elevation Model (DEM; Natural Resources Canada, 2024; <https://open.canada.ca/data/en/dataset/7f245e4d-76c2-4caa-951a-45d1d2051333>).

2.3. Individual Behaviours tested

We tested a total of 24 individual behaviours that potentially varied

within and between caribou groups during biologically relevant seasons (Table 1). Biologically relevant seasons for caribou were defined following Dyer et al. (2002), Wittmer et al. (2006), and McDevitt et al. (2009) (see Table A 2 for date ranges), and when appropriate, seasonal behaviours were extracted following these dates. A rutting season location was assigned to each collared caribou, and was estimated in one of three ways based on the number of GPS fixes available over that period: 1) > 15 GPS fixes: location estimates as the centroid of the 5 %-fixed-kernel isopleth (calculated using the function 'hr_kde' in the 'amt' package, version 0.2.1.0 in R-Studio, version 4.2.2, keeping all default values; Worton, 1989, Signer et al., 2018), 2) <15 GPS fixes available: the centroid of the minimum convex polygon (MCP; Worton, 1995) (using the R package 'amt'), 3) < 2 GPS points available: the average location. We only included individuals for which we could estimate a rutting location, and with at least 15 fixes/locations during the summer, winter, and calving seasons within the same calendar year. Each individual therefore had a minimum of 47 locations per year (DeCesare et al., 2012; Theoret et al., 2022). Another variable that has been shown to be significant for caribou is the elevation of rutting areas (Edmonds, 1988). Thus, elevations of rutting areas were collected as the average elevation of all locations used during the rutting period. While other wild ungulates, such as deer and moose, usually disperse as juveniles (Bunnell and Harestad, 1983; Hundertmark, 1998), caribou calves typically remain within their natal range for 6–24 months before gradually establishing a stable home range (Lesmerises et al., 2013; van Oort et al., 2011). As this study necessitated focusing on established home ranges, and the aim was to evaluate potential intra-specific units that may be used to inform conservation, we included only the last full year of telemetry data for adult individuals who were monitored for multiple years.

We calculated path lengths (m) within the calving season and period of movement from rutting areas to winter ranges as the sum of the distance between all successive GPS fixes. We delineated seasonal range polygons as the 100 % minimum convex polygons (MCPs, Worton, 1989, Nilsen et al., 2008) around the locations for each individual within each season (winter, summer, and calving), to compute both the area (km²) and perimeter (km). Indices of shape were calculated as the ratios between perimeter and area of the 100 % MCP (km/km²), where higher values indicate a more complex or irregular home range shape (i.e. the length of the edge within the landscape increases), suggesting that the animal's movement within its range is more fragmented. Indices of elongation were calculated as the ratio of 100 % MCP perimeter (km) to the perimeter of a circle having the same area as the MCP (km), where higher values indicate that the home range is more elongated or irregular, implying that the animal's movement within its range is more spread out (Moser et al., 2002). Seasonal changes in elevation use have also been hypothesized to be an important behavioural adaptation for some groups as a predator avoidance tactic (for example, during calving and altitudinal migration), or to access different food sources, such as arboreal lichen during times of high snow accumulation (Apps et al., 2001a, 2001b, Blagdon and Johnson, 2021, Cavedon et al., 2022a, 2022b, Theoret et al., 2022). We therefore calculated the absolute difference between the average summer and winter elevations (m.a.s.l.) for each individual. During the period of movement in the fall, we calculated the absolute range in elevation of all locations to capture altitudinal movements from rutting grounds to winter ranges.

To evaluate whether animals were migratory or sedentary, the index of overlap (IO; Eq. (1)) was calculated between winter and summer ranges frequented by individual caribou. Individual seasonal ranges were obtained by calculating the 95 % fixed-kernel isopleth, using the function 'hr_kde' in the R package amt (keeping all default values; Worton, 1989, Signer et al., 2018) if sufficient data was available (i.e. ≥15 GPS fixes). The resulting IO ranges from 0 to 1, where higher and lower values indicate resident and migratory behaviour respectively, following McDevitt et al. (2009):

Table 1

List of variables, types, and abbreviations used for identifying behavioural differences of woodland caribou in western Canada.

Variable type	Abbreviation	Variable	
Calving	CD	Calving date: predicted date of calving event based on movement rates.	
	Home range size and shape	CA	Calving area: area of the 100 % minimum convex polygon (MCP) (km ²) for the calving season
		CP*	Calving perimeter: perimeter of the 100 % minimum convex polygon (MCP) (km) for the calving season locations
	CMS	Calving MCP shape: ratio of MCP area to circumference of circle having the same area as MCP for calving season locations.	
	CER	Calving edge to area: ratio of the MCP perimeter to MCP area for calving season locations.	
	SA	SA	Summer area: area of the 100 % minimum convex polygon (MCP) (km ²) for summer ranges
		SP*	Summer perimeter: perimeter of the 100 % minimum convex polygon (MCP) (km) for the summer season locations
	SMS	Summer MCP shape: ratio of MCP area to circumference of circle having the same area as MCP for summer season locations.	
	SER*	Summer edge to area: ratio of the MCP perimeter to MCP area for summer season locations.	
	WA*	Winter area: area of the 100 % minimum convex polygon (MCP) (km ²) for winter ranges	
	WP*	Winter perimeter: perimeter of the 100 % minimum convex polygon (MCP) (km) for the winter season locations	
	WER	Winter edge to area: ratio of the MCP perimeter to MCP area for winter season locations.	
	WMS	Winter MCP shape: ratio of MCP area to circumference of circle having the same area as MCP for winter season locations.	
Location	RE	Rutting elevation: average elevation of all locations during the rutting period	
	CC(%)	Canopy cover at calving: percent canopy cover of average location on date of predicted calving	
	CE*	Calving elevation: Average elevation of all locations during predicted calving event (based on movement) over a 3-day window starting the date of a hypothesized calving event.	
	La	Latitude: average latitude of all locations within the 5 % MCP during the rutting season	
Movement	Lo	Longitude: average longitude of all locations within the 5 % MCP during the rutting season	
	MD	Movement distance: sum of the distance (m) between successive animal locations during the period of movement from rutting ranges to winter range	
	MED	Movement elevation difference: difference in elevation from rutting to winter ranges	
	M(IO)	Elevation range: absolute difference in elevation between average winter locations and average summer locations	
	ER		
CEG	Calving elevation gain: net change in elevation from late winter locations to calving locations		
CPL	Calving path length: sum of the distance (m) between successive animal locations during the calving season		

* Indicates variable excluded from statistical analysis due to concerns of collinearity, tested using variance inflation factors in the "usdm" package in R Studio (version 1.1–18, Naimi, 2015).

$$IO = \left[\frac{2A_{12}}{A_1 + A_2} \right] \quad (1)$$

where A_{12} is the area of overlap (km^2) of the summer and winter 95 % isopleths, and A_1 and A_2 are the areas (km^2) of the summer and winter 95 % isopleths for the animal.

Since woodland caribou ecotypes have previously been differentiated based on calving strategies (Bergerud, 1988), we analyzed movement and locations used during calving. According to the literature, woodland caribou typically calve between 15 May – 30 June (DeCesare et al., 2012; DeMars et al., 2013; Ferguson and Elkie, 2004a; McDevitt et al., 2009). To ensure we did not miss any potential calving events outside of this range, we included all movement from 1 May – 15 July to infer parturition. Parturition can be estimated through decreases in movement during the calving season (DeMars et al., 2013; Ferguson and Elkie, 2004a; Pond et al., 2016). Drops in daily movement rates to $<500 \text{ m} / 15 \text{ h}$ (20 m / hour) for at least three days has been identified as a reasonable estimation of a calving event (Pond et al., 2016). Therefore, following Pond et al. (2016), we defined movements $\leq 500 \text{ m} / \text{day}$ for ≥ 3 days in the spring to indicate a calving event. This provided estimates of calving dates as early as 17 May, and as late as 30 June.

Caribou ecotypes have been hypothesized to minimize predation at calving through selection of specific habitat features such as higher elevations or greater canopy cover (Bergerud et al., 1990; Bergerud and Page, 1987; Fancy and Whitten, 1991; Nobert et al., 2016). We extracted the average canopy cover at all locations used during estimated calving events for each individual (data obtained from Oduro Appiah et al., 2021). Additionally, differences in elevation use between late winter (22 February– 30 April; Ferguson and Elkie, 2004a, 2004b) and calving were calculated to evaluate whether individuals moved from lower to higher elevations to calve (a potential anti-predator strategy; Gustine et al., 2006; Pinard et al., 2012; Blagdon and Johnson, 2021). This resulted in a total of 24 discriminatory variables (Table 1) collected at the individual level.

2.4. Statistical analysis

To avoid multicollinearity among the variables mentioned above, we calculated the Variance Inflation Factors (VIF; (Zuur et al., 2010). Using the function 'vifstep' in the R package 'usdm' (version 1.1–18, Naimi, 2015) we carried out a stepwise selection analysis in which variables were removed until the highest VIF value was <3 (Zuur et al., 2010). Seven discriminatory variables were removed due to collinearity issues (MCP perimeter in all seasons -winter, summer, and calving, summer MCP edge:area ratio, winter area, calving elevation, and annual path lengths). The 18 remaining behavioural variables were then scaled and centred around the mean using the 'scale' function in base R. This allows uniformity and comparability across different behavioural measurements (Becker et al., 1988).

We applied a model-based cluster analysis to identify distinct behavioural patterns and delineate potential discrete intra-specific units. Model-based clustering is an unsupervised machine learning approach with several advantages, in that clusters are permitted to have different volumes, shapes, and variance structures (Bruce et al., 2020; Grün, 2019). We tested for the presence of clusters using the function 'Mclust' in the R package 'mclust' (version 6.0.0; Scrucca et al., 2016) with default parameters. The Mclust function uses finite Gaussian mixture models, which assume a multivariate Gaussian distribution for each component. These models result in ellipsoidal clusters centred at the mean of each component. While the clusters are centred at the mean, these models allow for flexibility in capturing the underlying data structure by accommodating different shapes and orientations of the ellipsoids around the mean (Scrucca et al., 2016). The 'mclust' package identifies the optimal number and assignment of individuals to clusters by iteratively fitting different multivariate distributions. This results in clusters that represent the allocation of individuals independent of a

priori cluster assignment (Scrucca et al., 2016). Models with 1–10 mixture components (or clusters) were fit, and Bayesian Information Criterion (BIC, Schwarz, 1978) was used to determine the most likely number of clusters. Evaluation of cluster results was achieved using the Davies-Bouldin index (DBI, Davies and Bouldin, 1979), which maximizes inter-cluster distance and simultaneously tries to minimize the distance between points in a cluster, resulting in a measure of the clustering performance. A lower DBI value (closer to 0) would indicate good separation and discreteness between clusters (Sætre et al., 2006).

Given the likelihood of correlated discriminatory variables, we conducted a principal component analysis (PCA) on cluster results. This approach allowed us to identify and visualize groups of correlated variables that consistently exhibit strong differentiation between potential behavioural clusters. The location an individual occupies is expected to significantly impact differentiation between potential clusters due to variation in the spatial structure of habitat patches, resources, and human disturbances across the study area. Therefore, we also investigated the index of spatial overlap between resulting behavioural clusters. This was achieved by evaluating the percent overlap in the 95 % KDE estimates, annually, and during the biologically relevant seasons described above, compared to the overall area (km^2) of the 95 % KDE for each cluster (Table A 3).

Finally, using a Random Forest (RF) analysis (Breiman, 2001; Cutler et al., 2007), we investigated the importance of discriminatory variables in accurately assigning individuals to identified behavioural clusters. RF models construct regression or classification trees by successively splitting the data based on predictors, fitting multiple decision trees to a dataset using bootstrapping, and then averaging predictions from all possible trees. An RF model was constructed using the function 'randomForest' in the homonymous R package (version 4.7–1.1, Breiman, 2001; Liaw and Wiener, 2002). This approach helps prevent any single predictor from overly influencing the decision-making process, resulting in more robust and accurate predictions (Kleanthous et al., 2020; Valletta et al., 2017). The algorithm randomly selects a subset of predictor variables for splitting at each node, preventing any single predictor from dominating the decision-making process. The RF model was constructed using 500 decision trees (see Fig. A 3), where the optimal configuration involved considering four variables at each split. Additionally, out-of-bag (OOB) predictions were used to assess the prediction accuracy of the RF model. During bootstrapping, a portion of the original dataset is left out at each iteration. These 'out-of-bag' points were then used to evaluate the model's performance, providing an independent and unbiased assessment of the prediction accuracy across the entire dataset. Accuracy and error rates are computed for each observation using OOB predictions and then averaged over all observations. Since OOB observations are not used in the tree fitting process, they provide a reliable measure of its performance across the dataset (Breiman, 2001; Cutler et al., 2007). Model training was achieved using the behavioural variables to predict cluster assignment. Optimization of the number of variables randomly sampled at each split was determined through tuning. This process involves a systematic exploration of different numbers of variables randomly considered for splitting at each node in the decision tree, iterating through 500 configurations, and highlighting the optimal number of parameters that maximizes the model's predictive power. The trained RF model was employed to predict cluster assignment, and model performance was evaluated through OOB error rates. Finally, the relative importance of discriminatory variables was predicted by assessing each predictor on model performance by estimating the Mean Decrease Accuracy (MDA, Genuer et al., 2010). MDA evaluates how the inclusion/exclusion of a variable affects the accuracy of the model. Therefore, higher values indicate that a variable is important in explaining or predicting the target outcome (Fox et al., 2017).

3. Results

3.1. Behavioural clusters found in caribou

The Bayesian Information Criteria (BIC) indicated that the Volume-Volume and Shape Identity (VVI) structure with six components (i.e. clusters) was the best-fitting clustering model for the behavioural dataset (Fig. 2). This model assumes the clusters have similar volumes, are roughly spherical in shape, and can have different orientations. This implies that identified clusters are expected to have similar spatial extents but may differ in spatial distribution or structure across the landscape. Therefore, the six identified clusters were based on differences in both presence and individual variation in measured behaviours. The DBI index resulting from the best fitting clustering solution (i.e. with six behavioural clusters) was 2.2, indicating relatively good separation and distinctiveness between clusters (see also Figs. 7–9 for visualization of specific behavioural differentiation across clusters). Individuals are classified into clusters to minimize differentiation without a priori groupings, and therefore, the six identified clusters represent individuals that show similarities (including presence/absence) in measured behaviours. The distribution of individuals among the six identified clusters showed that pre-defined sub-population units were not uniformly assigned to a single behavioural cluster but were sometimes distributed across multiple clusters (Table 2).

PCA analysis of cluster results allowed for the interpretation of behaviours driving differentiation between clusters, with the first and second components accounting for 26.4 % and 14.4 % of the variance,

respectively (Fig. 3). As anticipated, the biplot of the loadings highlights the significance of the spatial correlation present within the data, indicating that geographical relationships may influence behavioural variation (Fig. 3). Variables that notably influenced PC1 were associated with home range size, shape, and utilization (Fig. A 3 A.). Conversely, PC2 was primarily influenced by variables related to location (such as rutting elevation) and migratory behaviours (see Fig. A 3 B.). Clusters 2 and 3 covered the most extensive geographic range throughout the study region (Fig. 6; see also Table A 4. Behavioural clusters appear to be structured by geographic location (Fig. 4), where significant overlap was present between the 95 % KDE of neighbouring clusters (Fig. 5, see also Table A 5), indicating substantial spatial overlap between clusters found in the same geographic area despite variation in cluster size.

3.2. Cluster characteristics

Behavioural differences between the six identified clusters were not based on a single trait but differences across a suite of traits (Fig. 7, Fig. 8, and Fig. 9). The OOB error rate was 11.59 %, signifying favourable model performance (Breiman, 2001; Cutler et al., 2007). The assessment of variable importance revealed that rutting elevation (m) significantly influenced the accuracy of predicting cluster membership, with an MDA value exceeding 35 (Fig. 6). Similarly, canopy cover (%) during hypothesized calving events, home range size and shape (including winter edge:area and calving area), and migration (specifically altitudinal migration) also showed considerable importance, each with an MDA value exceeding 20 (Fig. 6).

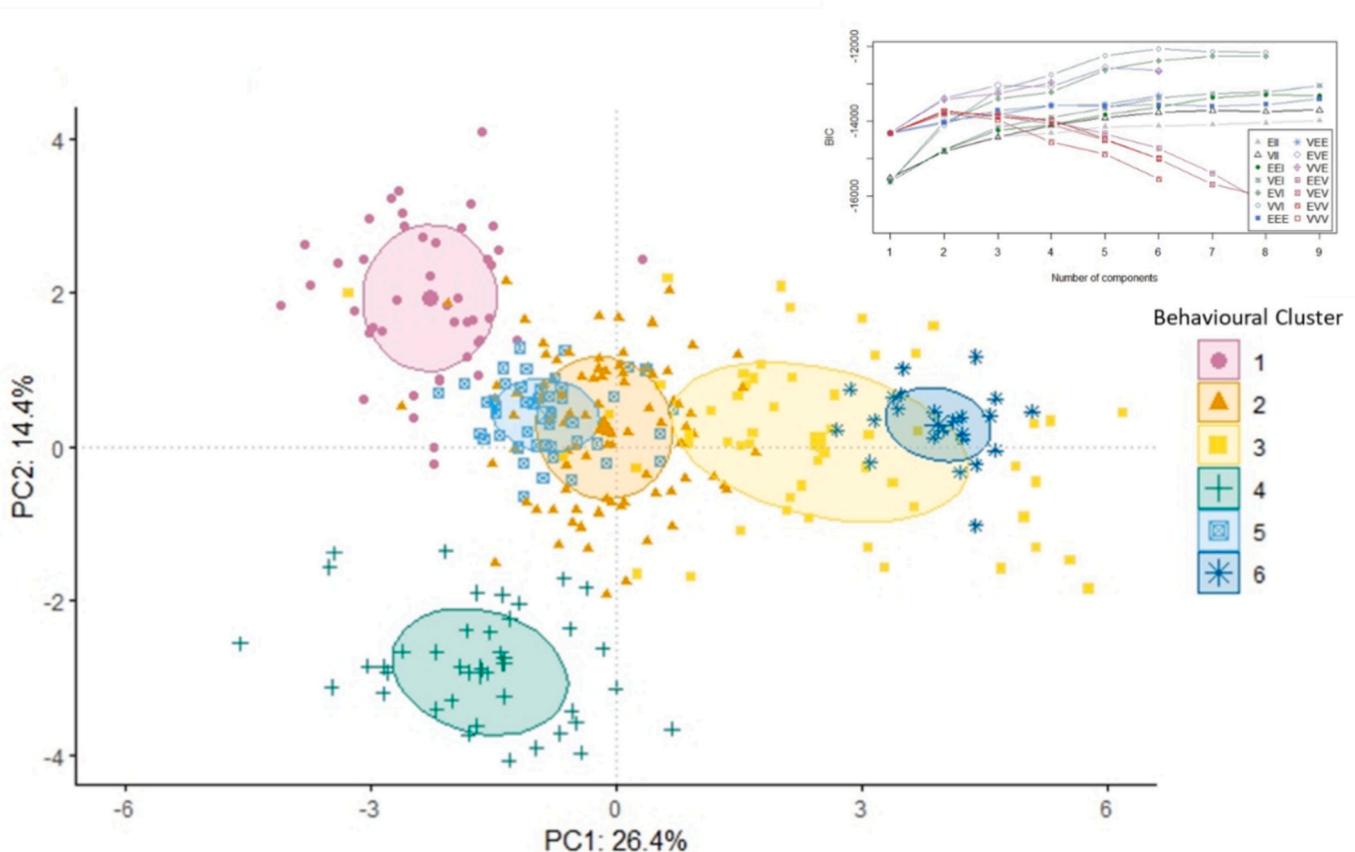


Fig. 2. Unconstrained multivariate Gaussian mixture model-based clustering resulting in six distinct behavioural clusters of woodland caribou throughout the province of British Columbia. Each point represents an individual caribou sampled across all 18 scaled discriminatory variables, with both shape and colour of the points representing identified behavioural cluster designation. Scaled discriminatory variables represent a total of 40.8 % of variation across the first two axes (26.4 % and 14.4 % on axis 1 and 2 respectively). The above model-based clustering assumes that datapoints are generated from a mixture of probabilistic methods, resulting in an optimal number of clusters of six ($G = 6$) based on model comparison of BIC values (mclust v6.0.0.; Scrucca et al., 2016).

Table 2

Percent of individuals belonging to behavioural clusters by population name. Included are also ecotype, designatable unit (DU), and SARA listing groups in different colours.*.**

Population	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	N*	Ecotype	DU	SARA Listing			
Calendar	0	0	0	100	0	0	5	Boreal	Boreal	Boreal			
Chinchaga	0	0	0	100	0	0	17						
Maxhamish	0	0	0	100	0	0	8						
Snake-Sahtaneh	0	0	0	100	0	0	12						
Westside Fort Nelson	0	0	33.3	66.7	0	0	6						
Barkerville	50.0	0	0	0	50.0	0	6				Mountain	Southern Mountain	Southern Mountain- Southern Group
Central Selkirks	100	0	0	0	0	0	5						
Columbia North	94.4	0	5.56	0	0	0	18						
Groundhog	100	0	0	0	0	0	2						
Hart Ranges	6.67	10.0	0	0	83.3	0	30						
Narrow Lake	0	0	0	0	100	0	1						
North Cariboo	16.7	8.33	0	0	75.0	0	12						
Purcells South	100	0	0	0	0	0	1						
Wells Gray North	22.2	22.2	11.1	0	44.4	0	9						
Wells Gray South	100	0	0	0	0	0	1						
Kennedy Siding	0	92.3	7.69	0	0	0	13	Northern	Central Mountain	Southern Mountain- Central Group			
Quintette	57.1	14.3	7.14	0	21.4	0	14						
Graham	0	100	0	0	0	0	4	Northern Mountain	Northern Mountain	Southern Mountain- Northern Group			
Itcha-Ilgachuz	0	0	11.5	0	0	88.5	26						
Telkwa	0	100	0	0	0	0	6						
Tweedsmuir	0	28.0	72.0	0	0	0	25						
Wolverine	25.0	75.0	0	0	0	0	4						
Atlin	0	0	100	0	0	0	10						
Carcross	0	0	100	0	0	0	1						
Finlay	0	100	0	0	0	0	1						
Frog	0	66.7	33.3	0	0	0	3						
Gataga	0	100	0	0	0	0	3						
Horseranch	0	0	100	0	0	0	2						
Liard Plateau	0	100	0	0	0	0	1						
Little Rancheria	0	0	100	0	0	0	3						
Muskwa	0	100	0	0	0	0	13						
Pink Mountain	0	95.0	5.00	0	0	0	20						
Rabbit	0	80.0	20.0	0	0	0	10						
Swan Lake	0	10.0	90.0	0	0	0	10						

* N represents the total number of individuals sampled per population.

** Each percentage is calculated as the proportion of that population belonging to the specific cluster.

Cluster 1 ($N_{\text{indiv}} = 44$, $N_{\text{pop}} = 11$) is characterized by smaller summer and calving MCP areas, coupled with the highest median MCP edge:area ratios among all clusters, with selection for canopy cover during calving and little to no elevational change from later winter habitats to high elevation calving areas. Cluster 1 contained notable variation in individual seasonal home range overlap with a mix of both true migrants ($IO = 0$) and sedentary ($IO = 1$) individuals, and evidence of altitudinal migration was observed. Cluster 2 ($N_{\text{indiv}} = 88$, $N_{\text{pop}} = 17$) demonstrated high winter MCP edge:area ratios and a preference for low canopy cover at calving, typically at high elevations, and variable IO values. Individuals in cluster 3 ($N_{\text{indiv}} = 56$, $N_{\text{pop}} = 5$) exhibited high indices of calving MCP shape, with larger calving MCP areas but small MCP edge:area ratios during this period than other clusters. Calving occurred at high elevations with movement from higher elevation winter grounds and notable differences in elevation between summer and winter ranges and in the movement period between rutting areas and winter ranges. In cluster 4 ($N_{\text{indiv}} = 46$, $N_{\text{pop}} = 5$), individuals have smaller summer and calving MCP areas than most other clusters, with greater calving MCP edge:area ratios and the earliest calving dates, selecting for more canopy cover at low elevations. Cluster 4 did not demonstrate evidence of altitudinal movement between summer ranges and showed the highest proportion of true sedentary individuals ($IO = 1$). Individuals classified into cluster 4 rutted at the lowest elevations compared to all other clusters. Cluster 5 ($N_{\text{indiv}} = 45$, $N_{\text{pop}} = 6$) is characterized by small calving and summer MCP areas with selection for the greatest median canopy cover at high elevations, with no notable changes in elevation between late winter and calving locations. Individuals displayed variable levels of migration, both in terms of IO values and altitudinal differences. Finally, cluster 6 ($N_{\text{indiv}} = 23$, $N_{\text{pop}} = 1$) is unique as it is comprised of individuals belonging to a single population unit (Itcha-

Ilgachuz; [British Columbia Caribou Recover Program, 2023](#)), where individuals were observed to occupy the largest summer and calving MCP areas and the smallest winter MCP areas. Individuals within this cluster rutted and calved at the highest elevations, with low levels of canopy cover at calving. Variable levels of home range overlap were observed within this cluster, with evidence of altitudinal migration observed through shifts in seasonal elevation (Figs. 7–9, Table A 3).

4. Discussion

As hypothesized, woodland caribou did not exhibit uniform behaviours across the study area. Instead, they displayed variability that could be categorized into six unique clusters based on patterns of movement, space use, and reproductive strategies (Fig. 4). Discriminatory variables that demonstrated high importance in accurately assigning individuals to clusters included rutting elevation (m), percent canopy cover at calving events (%), and total area (km^2) of the 100 % MCP of individuals during the calving season (Fig. 6, see also Figs. 7–9). These clusters represent the phenotypic diversity of woodland caribou in Western Canada, which could be used to help inform the delineation of intra-specific units for conservation. Our clustering results notably differ from currently defined federal intra-specific units for conservation (SARA, 2014), as well as proposed DUs often used to group caribou populations (COSEWIC, 2011). These discrepancies highlight the need for a more holistic approach in delineating intra-specific units for conservation. Comparing differentiation across various lines of evidence rather than focusing solely on differences between predefined units, such as geographic populations, enables the identification of potentially evolutionarily distinct units, accounting for the broader diversity present within the species (Grady and Quattro, 1999; Price et al., 2003).

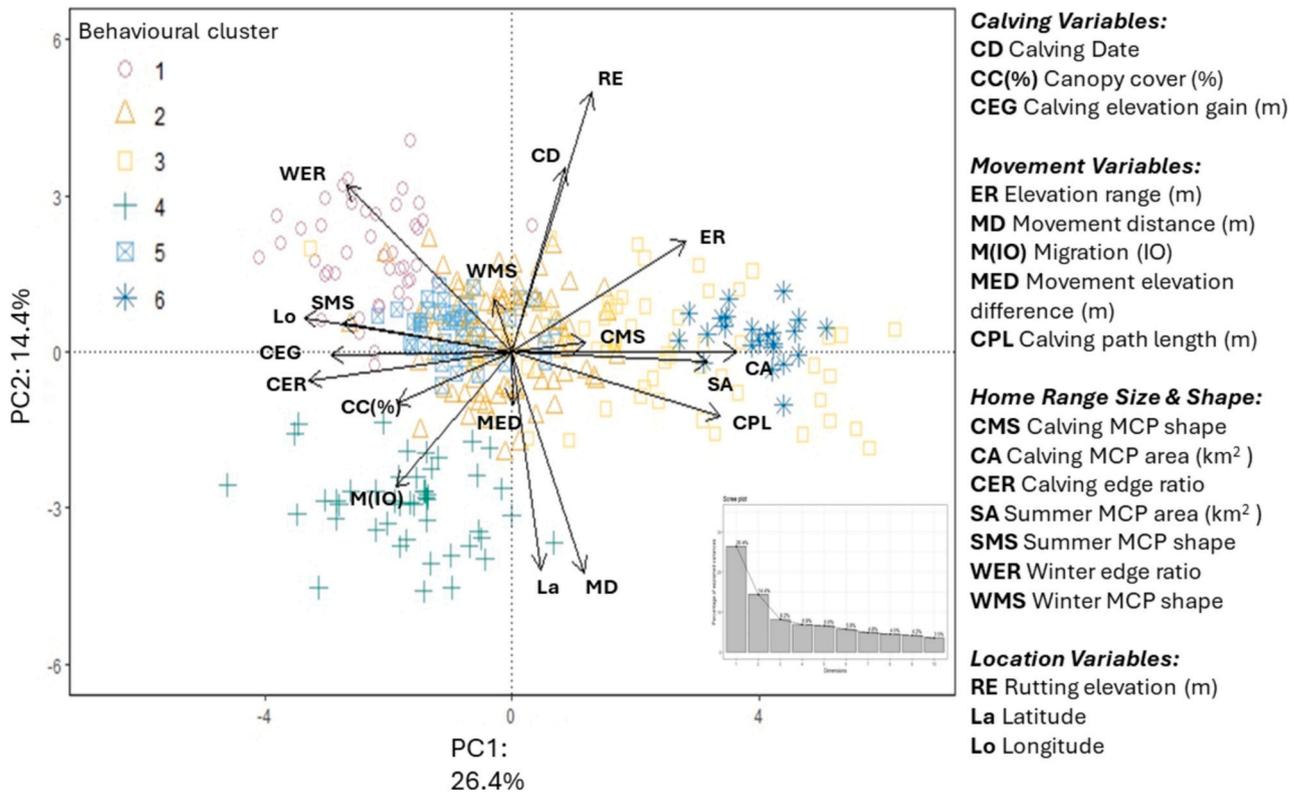


Fig. 3. Variable loadings and component scores for the first two components of the PCA of woodland caribou behavioural clusters discriminatory variables throughout British Columbia. Points represent individual caribou observations, with both colour and shape representative of behavioural cluster designation (1–6). Scaled discriminatory variables represented a total of 40.8 % of variation across the first two axes (26.4 % and 14.4 % on axis 1 and 2 respectively), with evidence of spatial structure apparent within cluster designation.

From a management perspective, it is essential to clearly define boundaries that may serve as repeatable units for monitoring and assessment purposes. Integrating behavioural information alongside conventional genetic and demographic criteria allow for more robust and ecologically meaningful population units that align with the practical requirements of managers. How individuals occupy and move through their environments has important consequences for the degree of mixing we may expect between populations (Morales et al., 2010). Understanding how individuals may differ in the way they occupy and move through their habitats allows for management action to be implemented across the entire movement path, as well as a better understanding of where and at what scale monitoring should take place (Allen and Singh, 2016). Overall, behavioural variation provides valuable insights into the ecological and evolutionary processes that shape population structure (Hawkes, 2009; Vasudev and Fletcher, 2015).

4.1. Behaviours driving differentiation of caribou groups

Movement to higher elevations has been hypothesized to be associated with potential increases in fitness through increased access to seasonal resources and a reduction in predation pressure (Hebblewhite and Merrill, 2007; Hsiung et al., 2018; Martin, 2015; Skutch, 1985). Caribou have also demonstrated high fidelity to various seasonal ranges, including both rutting (breeding) and calving areas (Cameron et al., 2020; Gunn and Miller, 1986; Popp et al., 2011; Wittmer et al., 2006). Specifically, migratory female caribou have been observed to display fidelity to rutting areas, at high elevations with gentle slopes (Gustine and Parker, 2008; Schaefer et al., 2000). This aligns with our observations that all clusters, with exception of cluster 4 where most individuals did not migrate, spent the rutting season at higher elevations. Fidelity to rutting areas may have strong impacts on the genetic structure of populations, contributing to reproductive isolation (Baker et al., 2013).

Rutting elevation not only aided in the differentiation of behavioural clusters, but served as a useful predictor in assigning individuals into their respective clusters, with an MDI exceeding 40 % (Fig. 6), likely reflecting habitat preferences and reproductive strategies.

Fidelity to calving areas has also been extensively documented within woodland caribou (Cameron et al., 2020; Nobert et al., 2016; Schaefer et al., 2000), with selection for calving grounds hypothesized to minimize predation rather than maximize forage availability (Gustine and Parker, 2008; Walker et al., 2021). Current intra-specific units for woodland caribou are often differentiated based on hypothesized anti-predator strategies at calving (Bergerud, 1988; Bergerud and Page, 1987; Pond et al., 2016). Previous literature has demonstrated that these strategies may include selection for mature closed-canopy forest stands at calving (Gustine et al., 2006; Lantin et al., 2003). Closed-canopy stands are characterized by dense lateral coverage, allowing for caribou to remain relatively inconspicuous, increasing safety of less mobile offspring (Courbin et al., 2009). Our analysis also revealed closed canopy cover as an important factor differentiating between identified clusters. Individuals classified into cluster 4 displayed the earliest hypothesized calving dates, at low elevations, and generally selected for intermediate values of canopy cover, with smaller calving ranges than other clusters. All other clusters spent the calving season at high elevations. However, unlike other migratory clusters, individuals classified into cluster 5 did not change elevation between late winter habitat and calving locations, selecting for areas with the highest median percent canopy cover to calve. Cluster 6 showed evidence of movement from high elevation late winter habitats to spend the calving period at median elevations >1800 m a.s.l., with low levels of canopy cover, consistent with behaviour previously observed from caribou in this region (Apps et al., 2001a). Behavioural variation in calving strategy is recognized as an important phenotype of adaptive significance for woodland caribou. Understanding the differences between potential intra-specific

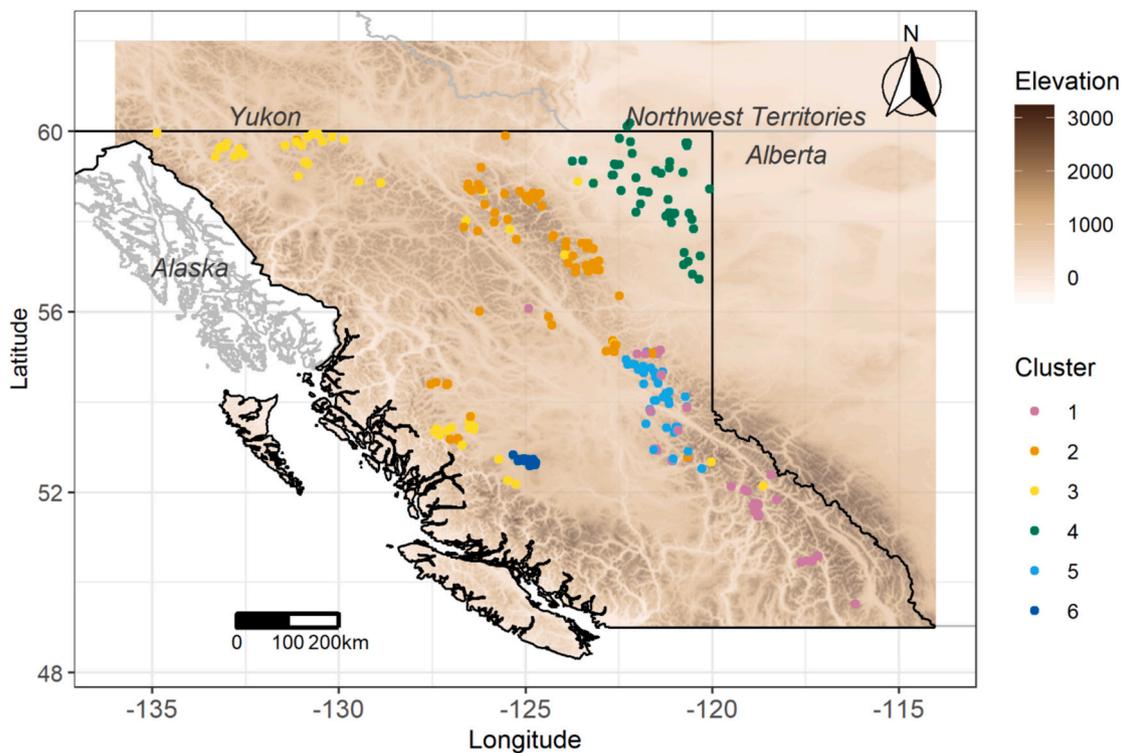


Fig. 4. Map of behavioural cluster designation for individual woodland caribou in the province of British Columbia. Each point represents an individual caribou, with colours representative of cluster designation based on the model-based Gaussian cluster analysis (mclust v6.0.0; [Scrucca et al., 2016](#)). Clusters therefore represent differences in timing and/or presence of measured behaviours across individuals. Location was estimated in one of three ways: 1) as the centroid of the 5 %-fixed-kernel isopleth during the rutting season when there was sufficient data available, 2) the centroid of the minimum convex polygon (MCP) during the rutting season when <15 GPS telemetry points were available, or 3) the 2-D average location when only 2 points were available during the rutting period.

conservation units can inform tailored management strategies to address the specific needs of populations, such as the conservation of old growth forests, allowing for increased canopy cover and travel routes between winter ranges and calving areas.

The area of the 100 % MCP (km²) during the calving season was also highly important in correctly classifying individuals, with a DBI > 25 % ([Fig. 6](#)). The shape and size of ungulate home ranges may be related to several factors, including reproductive status, habitat availability, local disturbances, available cover, or snow depth ([Brown et al., 2003](#); [Burt, 1943](#)). Furthermore, range size may reflect factors that could limit survival, such as predation ([Johnson et al., 2001](#); [Wilson et al., 2019](#)). In woodland caribou, winter and summer ranges are typically larger than calving ranges, where females are hypothesized to trade off forage quality and predation pressure ([Brown et al., 2003](#)). Moreover, calving and post-calving range sizes may reflect the limited movement of females with calves ([Rettie and Messier, 2001](#)). This is consistent with our results, where calving ranges were smaller than home ranges (represented by the 100 % MCP) during all other seasons. Cluster 3 and Cluster 6 were unique, with the largest median calving ranges compared to other clusters. These clusters also displayed more elongated or irregular ranges, implying movement within calving ranges was more dispersed ([Moser et al., 2002](#)). It is also worth noting that individuals classified in cluster 4 displayed the highest edge:area ratios during the calving season, implying the presence of fragmentation within their range, consistent with previous evidence from this area ([Faille et al., 2010](#); [Pinard et al., 2012](#)).

Another behaviour frequently used to group intra-specific units for woodland caribou is migration. Within our analysis, migration significantly contributed to PC2, which accounted for 14.4 % of the observed variation ([Fig. 3](#)). Unlike barren-ground caribou (*R.t. groenlandicus*), woodland caribou do not undertake extensive winter-summer migrations; however, they do exhibit both planar and altitudinal seasonal

range shifts to access seasonally available forage while minimizing predation ([Ferguson and Elkie, 2004b](#); [Fryxell and Sinclair, 1988](#)). It is important to note that seasonal range shifts are not always clear-cut (i.e. IO of 0 or 1), with some individuals displaying only small range shifts ([Cavedon et al., 2022b](#); [Theoret et al., 2022](#)). [Theoret et al. \(2022\)](#) highlights the importance of accounting for individual variation in migratory behaviour among woodland caribou, as well as differences in elevation of seasonal ranges. Furthermore, [Stamps \(2016\)](#) highlights that individuals within a population may not adhere to a single seasonal movement behaviour throughout their lifetime.

Knowledge of current caribou DUs in western Canada shows that individuals within a population may not adhere to a single seasonal movement behaviour throughout their lifetime, indicating plasticity in migration patterns ([Blagdon and Johnson, 2021](#); [Stamps, 2016](#); [Theoret et al., 2022](#)). We observed a high proportion of clear migrants (IO = 0) in cluster 3, whereas individuals in cluster 4 displayed a high proportion of clear sedentary behaviour (IO = 1). Individuals within other clusters displayed a wide range of overlap between seasonal ranges, with varying proportions of migratory and sedentary individuals ([Fig. 8](#)). Evidence of altitudinal separation of seasonal ranges was observed within all clusters with exception of cluster 4. It is worth noting that individuals classified as cluster 5 showed little differences in mean elevation between winter and summer ranges, with a median difference of |47.3| m a.s.l. However, individuals within this cluster did display the highest median change in elevation during the period of movement between the rutting season and winter, supporting previous work highlighting the plasticity in seasonal movement behaviours within caribou from the southern mountain-central and southern groups (or central and southern mountain; DU 8 or DU 9, [Theoret et al., 2022](#)).

Our analysis focused on female woodland caribou due to provincial government protocols prioritizing their monitoring for conservation, as well as their roles in defining seasonal movements and habitat fidelity

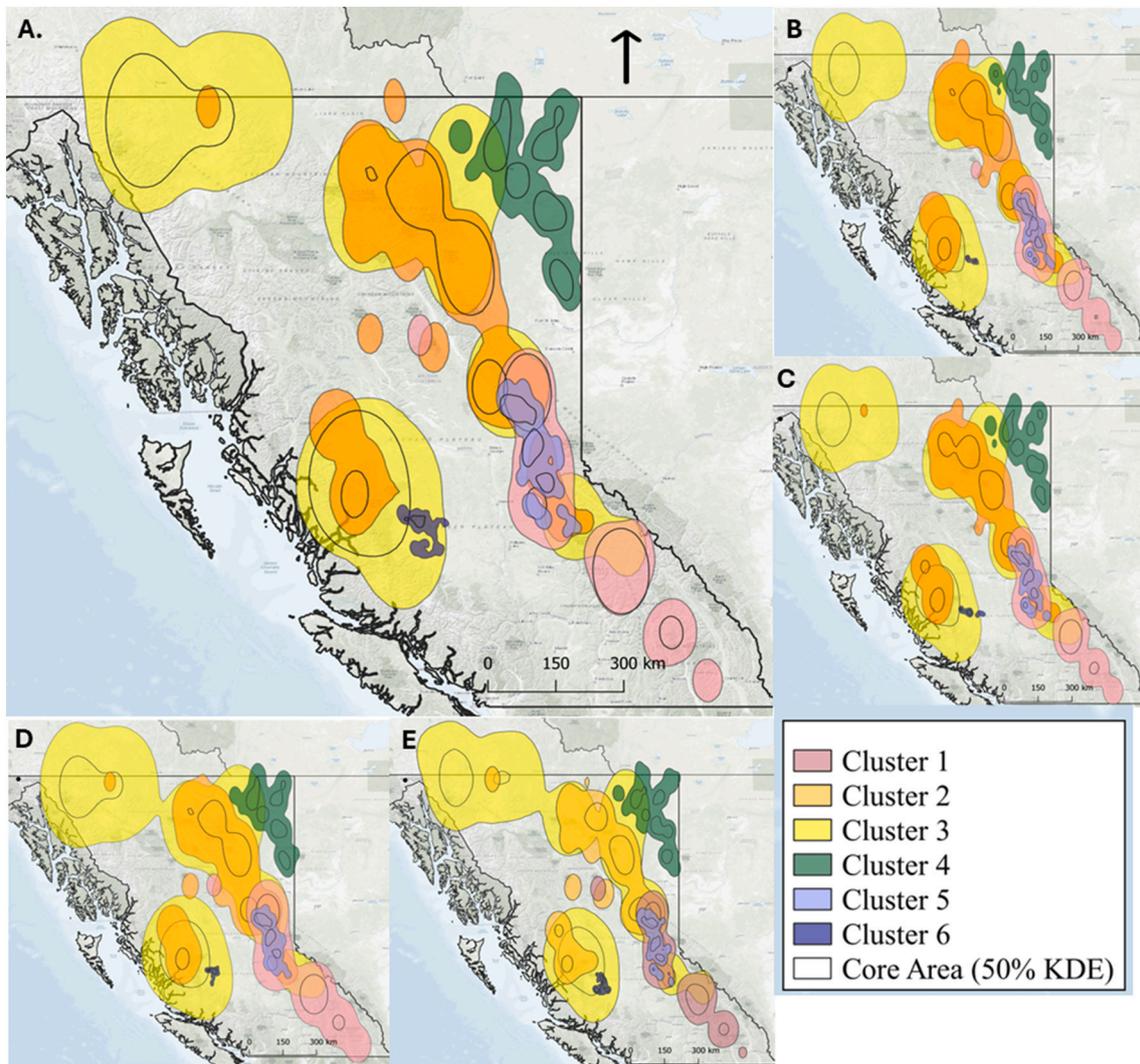


Fig. 5. Cluster ranges represented by the 95 % KDE for female woodland caribou throughout British Columbia A. Annually, B. during the calving period (15 May – 30 June), C. summer (1 July – 15 September), D. rutting period (or breeding, 16 September – 15 November), and E. winter (1 December – 30 April). Core areas were computed through the 50 % KDE for all clusters. See Table A4 and S 5 for % overlap between cluster ranges seasonally.

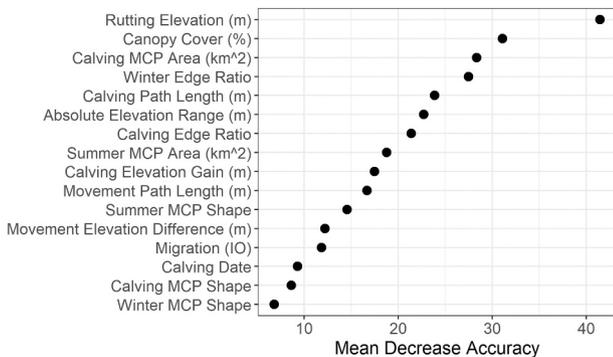


Fig. 6. Importance of behavioural discriminatory variables in the clustering of woodland caribou in western Canada based on Random Forest (RF) models. Mean Decrease Accuracy evaluates how the inclusion/exclusion of variables impacts model performance. The RF model had an Out of Bag error rate of 11.59 % indicating overall good predictive power. Rutting elevation (m), canopy cover at calving (%), and calving MCP area (km²) were most important in prediction accuracy of the RF model.

(Bergerud et al., 2008; McDevitt et al., 2009). However, it is crucial to acknowledge that males exhibit distinct movement patterns and habitat preferences which can significantly contribute to population connectivity and gene flow and should therefore also be considered in conservation efforts and the delineation of intra-specific units (Debeffe et al., 2019; Ferguson and Elkie, 2004a; Jakimchuk et al., 1987; Nicholson et al., 2016). Males may mate in adjacent units (Lent, 1965), facilitating gene flow between neighbouring populations and across the landscape, potentially impacting behaviours with a genetic basis. In ungulates, maternal care has been shown to be significant in determining behaviours that may be socially learned by offspring (Lent, 1974), and in this study we address the current landscape of female behavioural clusters. Future efforts should aim to incorporate behaviours and movement of males to obtain a more comprehensive understanding of sex-based differences and conservation needs.

4.2. Spatial distribution of behaviourally differentiated caribou groups

As predicted, the location an individual occupied seemed to influence clustering results (Fig. 4). Cluster 1 is situated in the southern region of British Columbia and extends into central part of the province, while cluster 2 ranges from northern British Columbia to the interior near the Nechako Plateau. Cluster 3 encompasses the widest

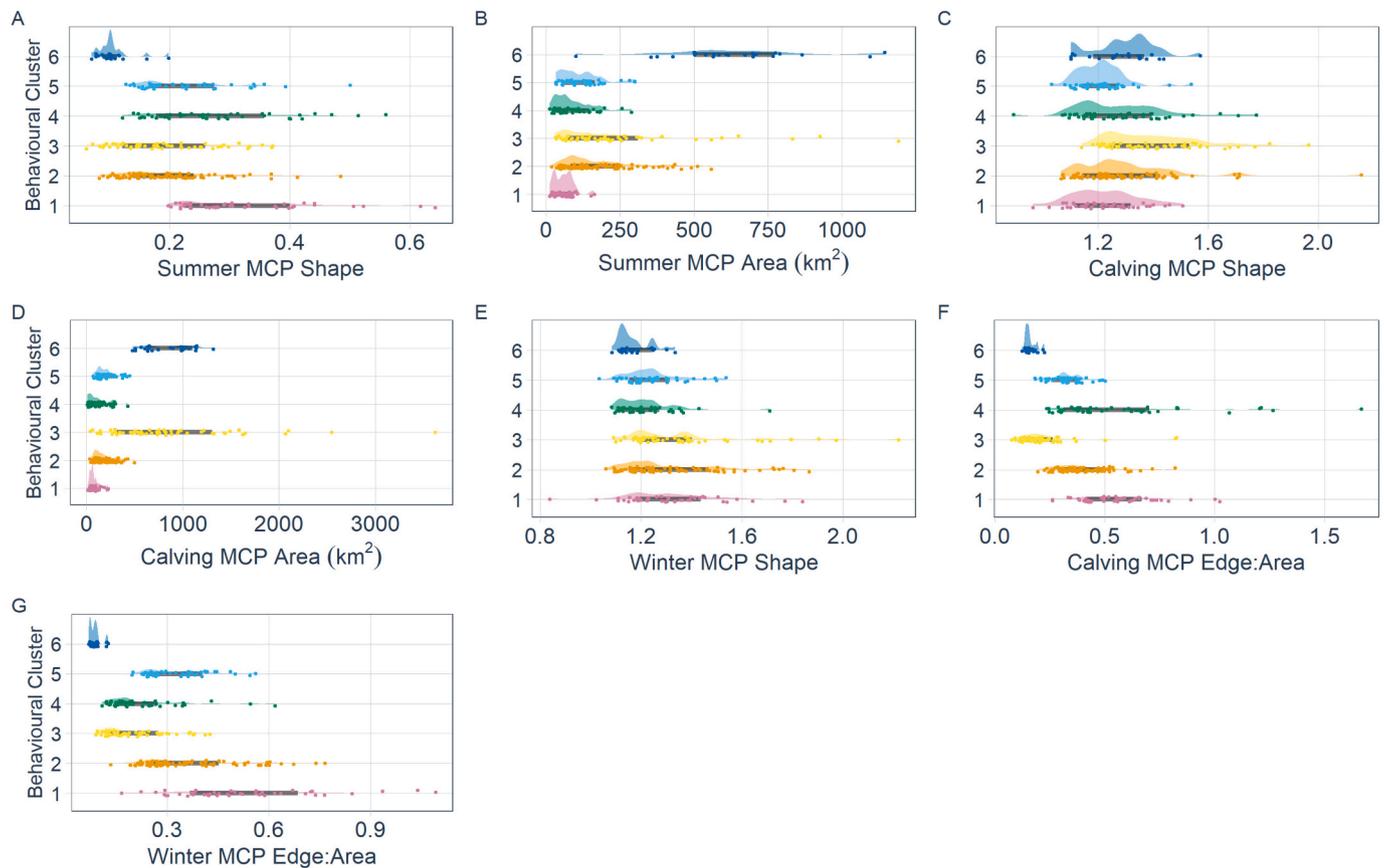


Fig. 7. Data structure of discriminatory variables related to measured metrics of space-use, visualized by behavioural cluster, where A. Summer, C. calving, and E. winter MCP shape, measured as the ratio of the 100 % Minimum convex polygon (MCP) perimeter (km) and the perimeter of a circle of the same area (km). Higher values would indicate that the home range is more elongated or irregular, implying that the animal's movement within its range is more spread out. B. Summer and D. calving 100 % MCP area (km²). F. Calving and G. winter edge:area ratio (km:km²), which is the ratio of the 100 % MCP perimeter to the area of the 100 % MCP. Higher values indicate a more irregular home range shape, implying that an animal's movement within its range is more fragmented. Colours correspond to identified behavioural clusters represented on the y-axis. Each point represents an individual caribou.

distribution, with individuals primarily located in northwestern and central (Nechako and Fraser Plateau) British Columbia, supplemented by some individuals in southern and northeastern regions. Cluster 4 is predominantly located in low elevations, in the northeast corner of the province, whereas cluster 5 is concentrated in central British Columbia. Finally, cluster 6 is exclusively located near the Fraser Plateau (Fig. 4). Spatial overlap observed between neighbouring clusters (Fig. 5) indicates geographic boundaries between clusters are not distinct. This suggests a dynamic landscape of behaviours, potentially driven by habitat use and availability (Semeniuk et al., 2012).

The six behavioural clusters identified in our results roughly align with current SARA designation for caribou intra-specific units with some notable differences (Fig. 1; SARA, 2014). The boundaries of inferred clusters show significant overlap, indicating the presence of transitional zones (Fig. 4 and Fig. 5). This is particularly obvious in central British Columbia, where northern, central, and southern DUs overlap in their distributions, rather than segregating based on current intra-specific units. Most boreal caribou were classified into cluster 4, which aligns with current knowledge of boreal space-use and movement behaviours (Briand et al., 2009; Ferguson and Elkie, 2004b), apart from two boreal individuals who were classified into cluster 3. These individuals were from the Westside Fort Nelson population, where indigenous traditional knowledge shared by Treaty 8 First Nations community members has reported movement into neighbouring mountain population ranges (Leech et al., 2016a, 2016b, K. Wolfenden, personal communication, December 2023). This has also been demonstrated by the long-distance movement from boreal caribou ranges into mountain ranges observed

from telemetry data (Watters and DeMars, 2016). Our present analysis shows spatial overlap between these cluster ranges beyond the individual scale annually (Fig. 5).

Finally, the most notable difference was the identification of a distinct cluster (cluster 6), exclusively comprised of individuals from the Itcha-Ilgachuz population unit. The exclusive presence of individuals from this population within cluster 6 is noteworthy, and mirrors preliminary genomic findings from the region (Michalak, 2023). The investigation of spatial dynamics, and the index of overlap between identified behavioural clusters suggests that behavioural differences are linked to their spatial distribution. Caribou behaviour may therefore be influenced by landscape features, where the observed overlap between neighbouring clusters (Fig. 5) indicates that behavioural variation exists both within and between populations (Table 2).

It is worth noting that variation observed in the spatial distribution of identified clusters (i.e. the geographic range of cluster 2 and cluster 3; Fig. 4 and Fig. 5) could be linked to translocation efforts throughout British Columbia. Within the province there is a long history of translocations of caribou as a method of population recovery (Boutin and Merrill, 2016; Jex, 2013; Kinley and Bio, 2010; Mathieu et al., 2022; Stronen et al., 2007). Movement of individuals between populations in British Columbia is reported as early as 1984 (Compton et al., 1995; Gordon, 2012; Mathieu et al., 2022; Young et al., 2001). Some examples of these include movement of individuals into the Telkwa range (Southern Mountain – Northern group, located in central British Columbia near the Nechako and Fraser plateau) using various source populations including Chase, Sustut (more recently referred to as

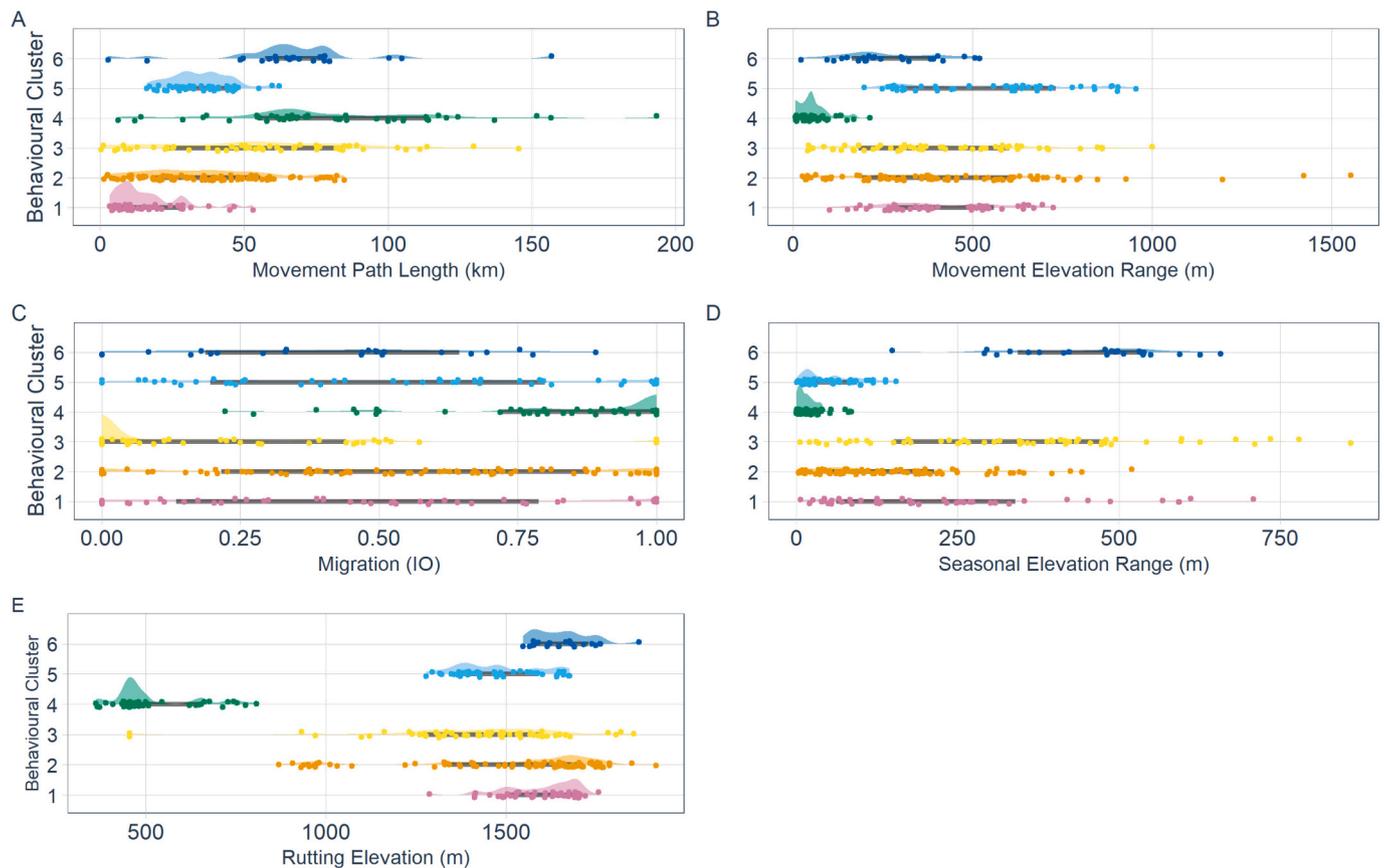


Fig. 8. Data structure of discriminatory variables related to measured metrics of movement, visualized by behavioural cluster, where A. Total path length (m) in the period of movement between rutting and winter periods. B. Absolute difference in elevation (m) between the average elevation recorded during the rutting to winter periods. C. *index of overlap* between summer and winter 95 % kernel density estimates (KDEs) within the same calendar year. IO = 1 indicates individual is sedentary, and IO = 0 indicates individuals are migratory. D. Absolute difference in elevation between the mean summer and winter elevation. E. Average elevation gain from locations in the 95 % summer KDE, compared to locations in the 5 % rutting KDE.

Thutade and Klinse-za), Burnt Pine, and Wolverine, belonging to the northern ecotype (Cichowski, 1996; Paterson and Ingebjorg, 2016; Stronen et al., 2007, H. Schwantje, personal communication, March 2024).

Translocation of animals throughout British Columbia could have consequences on both behavioural and genetic variation and could account for the geographic range observed for cluster 2 and cluster 3. Specifically, recent movement of individuals into the Telkwa range was achieved using animals that would have been found within the geographic boundaries of both cluster 2 and 3, offering one potential explanation for the geographic overlap between these two clusters within that region (Fig. 5). In previous studies, evaluation of post-release behaviour of an alpine ungulate (ibexes; *Capra ibex ibex*) have shown that there is a period of instability of movement behaviours in translocated individuals. It was hypothesized that social behaviour played a key role in the adaptation process of translocated individuals to the new area (Scillitani et al., 2012). Other studies have also evaluated the propensity of ungulate migration of translocated individuals, suggesting that learning and social transmission are the primary mechanisms by which migration evolves (Jesmer et al., 2018). Caribou display fission-fusion group dynamics (Body et al., 2015), where previous landscape knowledge has been shown to be important in movement decisions (Lesmerises et al., 2018). However, outcomes of successful translocation efforts for caribou in British Columbia are not well documented within the literature.

4.3. Ecology and conservation of differentiated groups

Phenotypic differentiation in behavioural traits plays a crucial role in understanding the adaptive potential and responses of populations to varying environmental conditions. Phenotypes serve as focal points for selection pressures and reflect the processes that contribute to species diversification. They offer insight into both the current and historical selective pressures populations face, holding information that may not be apparent in the genome (Zamudio et al., 2016). Selective pressures that populations face also vary temporally and geographically, altering the fitness of phenotypes across the landscape (Paz et al., 2015; Wang and Bradburd, 2014). Phenotypic variation can therefore be a precursor to genetic differentiation (Ortego et al., 2015), and in combination with genetic data can be used to help infer patterns of local adaptation (McKay and Latta, 2002). From a conservation standpoint, strong phenotypic divergence indicating the presence of local adaptation could guide management actions aimed at preserving populations with unique evolutionary trajectories (Crispo, 2008; Fraser and Bernatchez, 2001; Moritz, 2002).

In addition to genetic factors, phenotypic clusters may emerge due to phenotypic plasticity, where individuals adapt behaviours to novel environments or conditions, leading to divergence favoured by selection (Price et al., 2003). This adaptive process allows individuals exhibiting plastic responses to gain fitness benefits (Sultan and Spencer, 2002), enabling rapid changes in behaviour despite the slower pace of genetic evolution (Bradshaw, 1965; Doebeli and Dieckmann, 2003). Moreover, anthropogenic disturbances and habitat fragmentation, common across British Columbia in varying severity, have been linked to demographic

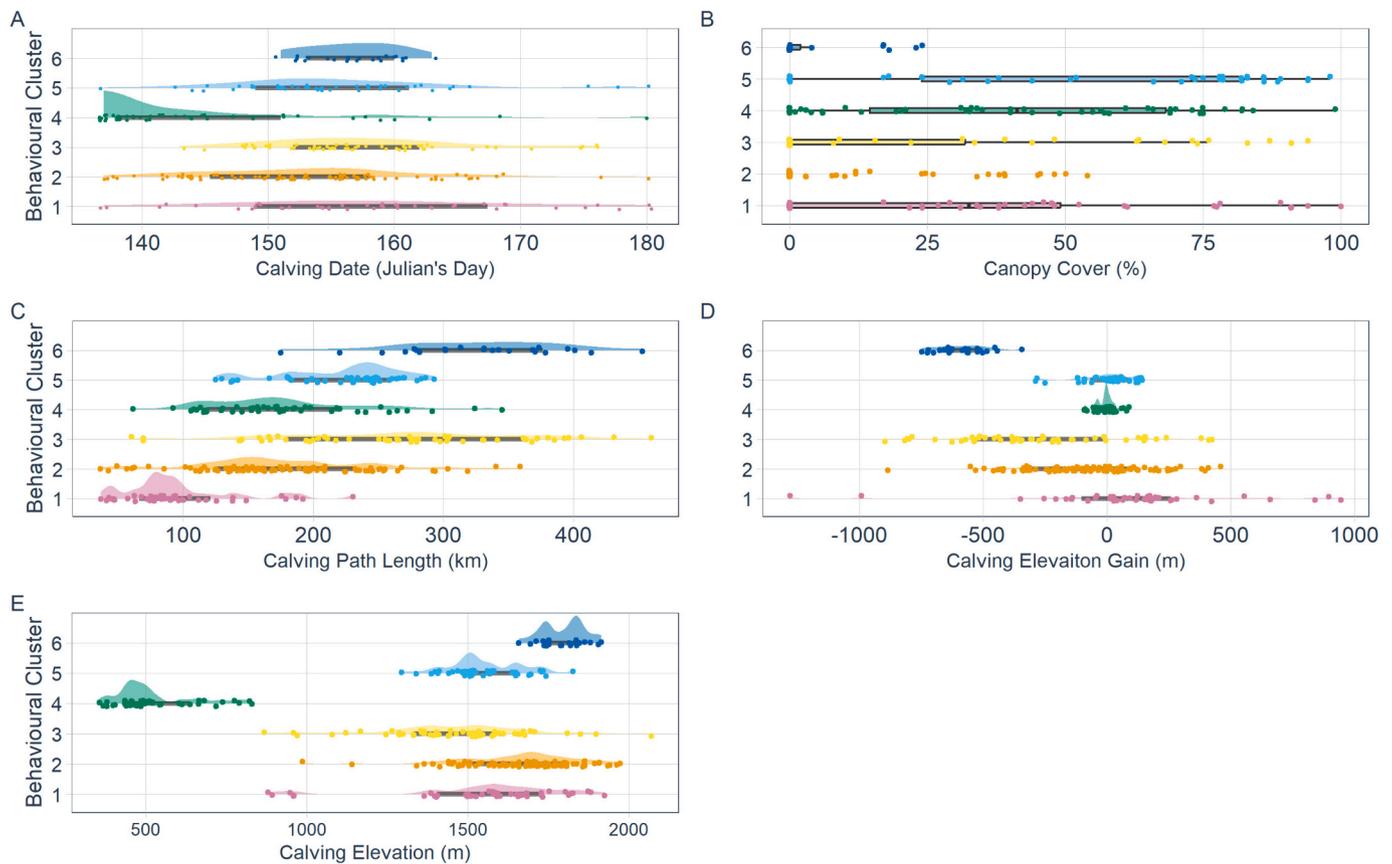


Fig. 9. Data structure of discriminatory variables related to measured metrics of movement and calving strategy, visualized by behavioural cluster, where A. is the hypothesized calving date (Julian's Day) based on a reduction in total daily movement ≤ 500 m for ≥ 3 consecutive days. B. Average canopy cover (%) of locations recorded during the hypothesized three-day calving window. C. Total path length (km) of successive locations recorded during the calving season. D. Calving elevation gained, as the difference in mean elevation used in late winter (22 February – 30 April) and the mean elevation during the calving season. E. Mean elevation of all locations used during the calving period. Due to collinearity issues, the absolute calving elevation was not included in clustering models but included to help interpret calving elevation gain. Colours correspond to identified behavioural clusters represented on the y-axis. Each point represents an individual caribou.

and evolutionary consequences, and leads to increased differentiation (both genetic and phenotypic) among populations, and decreased within-population diversity (Ortego et al., 2015).

In gregarious species, behaviours are also transmitted through social learning, shaping group-specific cultures. This may lead to distinct, reproductively isolated populations occupying the same geographic area (Whitehead, 2010; Whiten, 2017). Social transmission, in conjunction with genetic determinism, is a fundamental mechanism that produces heritable behaviour (Jesmer et al., 2018; Whitehead et al., 2023). Information and behaviour can be acquired through learning from a parent or shared by members of a community (both vertical and horizontal transmission of behaviours; Whitehead et al., 2019; Whitehead and Rendell, 2014; Whiten, 2017). Therefore, behavioural phenotypes may be similar between individuals but vary between communities of individuals, justifying the use of behavioural patterns as a method to delineate intra-specific units which may be evolutionarily important (Whitehead et al., 2023). Since behavioural variation can be learned from a range of individuals, it can therefore evolve similarly to genes. Individuals within a population can modify socially learned traits before exhibiting them to others (Whitehead et al., 2019). These traits can then impact demographic or ecological patterns in a way that significantly alters the evolutionary trajectory of the population (Ramsey, 2013; Richerson and Boyd, 2008; Whitehead et al., 2019), which for example has been demonstrated in foraging behaviour (Slagsvold and Wiebe, 2011), recognition and detection of predators (Curio et al., 1978; Griffin, 2004), and migration (Jesmer et al., 2018; Nelson, 1998).

4.4. Conclusion and conservation applications

Delineating evolving populations into discrete units and ecotypes is complex, yet critical for the effective use of conservation resources, as broad species-level classification may miss critical intra-specific variation necessary for maintaining adaptive potential and biodiversity (Clark et al., 2011; Mee et al., 2015; Morrison, 2012; Weckworth et al., 2018). In this study, analysis of individual variation in movement behaviour could be used to reveal unique intra-specific units for caribou in western Canada. We identified six clusters of caribou based on individual behavioural variation, where elevation of areas used during rutting, canopy cover (%) and home range size at calving, and migratory behaviour were significant in differentiating between clusters.

Phenotypic variation (both genetic and ecological) can shape ecosystem dynamics by structuring communities, enhancing demographic resilience, and increasing evolutionary potential through the diverse ecological roles individuals and populations fill (Hughes et al., 2008; Jump et al., 2009). Traditionally, intra-specific units for conservation have been identified using genetic data or a priori groupings (Avice, 2005; Coates et al., 2018). However, these approaches may fail to capture critical phenotypic and ecological variation that arises through mechanisms such as local adaptation and selection (Hughes et al., 1997; Violle et al., 2012). In addition, intra-specific variation, particularly when it manifests as distinct behavioural phenotypes, has the potential to generate significant ecological impacts and factor into ecosystem functioning (Des Roches et al., 2018; Hendry, 2016). While caribou exemplify the complexity of defining intra-specific units for

conservation, this study establishes a framework for the definition of ecotypes across terrestrial species and systems, and the delineation of biologically meaningful ranges that can guide habitat protection and restoration efforts. Then, habitat restoration, even if designed to be species specific, may benefit other species in the ecosystem (Finnegan et al., 2018).

Our findings indicate a path to protect behavioural diversity within species in general, as intra-specific variation plays a key role in their adaptive potential and resilience to environmental change (Found and St. Clair, 2016; Whitehead et al., 2023), offering actionable insights for conservation managers. Our methodological approach is spatially explicit and provides, as outputs, ranges where behavioural clusters occur. These same ranges would be ideal locations for protected areas, in case the ecological variants that are detected are considered by societies a conservation priority (as is the case for caribou and as could be the case for other terrestrial species). Furthermore, the ecotypes that are determined with this methodology can inform selection criteria for reintroduction and translocation efforts, using individuals ideally of the same ecotype and therefore likely suited to the release environment, enhancing survival and integration potential (Jesmer et al., 2018; Sciliani et al., 2012). For example, caribou individuals belonging to mainly migratory ecotypes should not be translocated in ranges of ecotypes that are mainly sedentary, or this will affect their survival (Compton et al., 1995). These management scenarios illustrate how the identification of intra-specific behavioural variation can be directly applied by agencies to improve conservation efforts.

Our approach provides a practical tool for defining ranges of conservation units for animals and for identifying ecotypes that reflect the ecological reality of intra-specific diversity. Conservation units identified through intra-specific variation across multiple phenotypic traits can serve as conservation focal points, also safeguarding the broader ecosystem and biodiversity by maintaining ecological relationships (Des Roches et al., 2018). Here, we demonstrated a new system to detect ecotypes, through focusing on intra-specific variation, highlighting the need to incorporate behavioural data into conservation planning to enhance the success of these efforts.

CRediT authorship contribution statement

Margaret M. Hughes: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Charlotte Bourbon:** Writing – review & editing, Methodology. **Pietro Milanesi:** Writing – review & editing, Validation, Software, Methodology. **Jasmine S.M. Veitch:** Writing – review & editing. **Samuel Deakin:** Writing – review & editing. **Helen Schwantje:** Project administration, Data curation. **Caeley Thacker:** Project administration, Data curation. **Agnès Pelletier:** Project administration, Data curation. **Jean Polfus:** Data curation. **Peter Neuhaus:** Writing – review & editing, Methodology. **Kathreen E. Ruckstuhl:** Writing – review & editing, Methodology. **Jocelyn Poissant:** Supervision, Funding acquisition, Conceptualization. **Marco Musiani:** Supervision, Funding acquisition, Conceptualization.

Research data for this article

Due to the sensitive nature of Species and Ecosystems Data, raw location data and information will not be shared publicly.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used Grammarly services to correct grammar and spelling and improve the clarity of some sentences. Additionally, ChatGPT was used to help correct code for data cleaning and figure creation using R-Studio. After using these tools, the author(s) reviewed the edited content as needed and take full

responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110933>.

Data availability

The authors do not have permission to share data but published the code on GitHub repository at <https://github.com/margarethughes95/Using-movement-to-inform-intra-specific-units-for-caribou->

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Glossary

Evolutionary Significant Unit (ESU): Groups of individuals of a species whose divergence can be measured or evaluated by putting differential emphasis on the role of evolutionary forces at varied temporal scales. Generally, ESUs are comprised of a population or groups of populations that are substantially reproductively isolated from conspecific units and represent an important component of the evolutionary legacy of

the species (Moritz, 2002, 1994; Ryder, 1986a, 1986b; Waples, 1998). ESUs are diagnosable based on concordant distributions or traits, such as genetic or ecological differentiation, and often arise from isolation (Ball et al., 2010; Crandall et al., 2000).

Designatable Unit (DU): Discrete and evolutionarily significant units (like ESUs) of the taxonomic species, where significance means the unit is important to the evolutionary legacy of the species as a whole and, if lost, would not be replaced through natural dispersion. Discreteness is based on evidence of heritable traits or markers that distinguish the putative DU from others indicating limited gene flow (or isolation), or natural geographic isolation between DUs that severely limits the transmission of information between them for a long time (COSEWIC, 2018).

Ecotypes: Groups of populations which are distinguishable by a composite of variation in many traits and allele frequencies over space. Ecotypes are the product arising as a result of adaptation to local environmental conditions leading to phenotypic differences (Gregor, 1944).

Conservation Unit (CU, also Management Unit; MU): Demographically independent sets of populations, characterized by limited gene flow, and can be managed to retain the larger ESU (Funk et al., 2012; Moritz, 1994; Palsbøll et al., 2007).