Investigating Flexible Migration in Hudson Bay Woodland Caribou (*Rangifer tarandus caribou*)

By

Alexis Pereira

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ABSTRACT

INVESTIGATING FLEXIBLE MIGRATION IN HUDSON BAY WOODLAND CARIBOU (*RANGIFER TARANDUS CARIBOU*)

Alexis Pereira	Advisor(s):
University of Guelph, 2023	Dr. John Fryxell

Facultative migration has been hypothesized as a strategy to optimize energetic gain in response to environmental fluctuations. The forest-tundra and forest-dwelling ecotypes of Ontario woodland caribou (*Rangifer tarandus caribou*) are often presumed to differ in migratory strategy, however their potential for facultative migration has yet to be explored. Understanding the inherent variation of migration could help improve habitat management. We compared GPS telemetry-based movement data from 109 radio-collared caribou across northern Ontario with estimates of vegetation, snow cover, and human disturbance to identify environmental drivers associated with migration. We also evaluated whether caribou exhibited a migratory syndrome, using measures of selection and movement in comparison with movement strategies. We found evidence of facultative migration from both ecotypes, with little evidence of an overlying migratory syndrome. Both probability and distance of migration were positively correlated with snow, while only probability increased with vegetation. Plasticity in migration may suggest resilience to change.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS, ABBREVIATIONS OR NOMENCLATURE

FD… Forest-dwelling (ecotype)

FT… Forest-tundra (ecotype)

NDVI… Normalized difference vegetation index

SWE… Snow water equivalent

1 Introduction

1.1 Flexibility in migration

Finding a consistent definition of migration is challenging due to the variability of what migration can look like, both across species and within a single population. Migration is broadly described as cyclical movement between separated, seasonal ranges (Fryxell and Sinclair 1988), which is a definition that encapsulates a diverse range of behaviours, from highly variable, short displacements (Hofer and East 1993), to unwavering, population-wide, cross-continental flights (Alerstam et al. 2003). Each definition can have its own ecological consequences, including facilitating energy transfer from different regions, altering interspecies and conspecific interactions, and increasing the likelihood of encountering anthropogenic disturbance (Milner-Gulland et al. 2011). In turn, the environment has strong effects on determining the extent of migration; conditions such as resource availability and competition can shape the time, duration, distance, and many other aspects of migration (le Corre et al. 2017, Gurarie et al. 2019). Both extrinsic and intrinsic factors interact to drive variability in migration, but the extent of influence by each factor on migration is highly variable across different species and not yet well understood (Berg et al. 2019).

Migration, particularly in ungulates, has historically been seen as an obligate behaviour that is genetically hardwired such that individuals consistently migrate every year, regardless of conditions, with little flexibility from year to year (Berthold 1991, Newton 2012, Cavedon et al. 2022). In some species, there is strong evidence to support that migration is strongly predetermined by genetic constraints (Salewski and Bruderer 2007, Klütsch et al. 2016). However, recent research suggests that ungulate migration is not always a static, defining trait, but rather a flexible, behavioural response to variable stimuli (Eggeman et al. 2016, Xu et al. 2021). Facultative migration describes an optional behaviour in which individuals demonstrate behavioural plasticity, choosing to migrate or not based on external conditions, such as weather and food availability; or internal factors, such as age (Newton 2012). Evidence of this more flexible form of migration is seen across many taxa, including birds, fish, and mammals (Newton 2012, Shry et al. 2019, Xu et al. 2021).

Variation in migration is tied strongly to an organism's environment, and the associated ecological costs and benefits of migration (Nicholson et al. 1997, Milner-Gulland et al. 2011). Migration is a costly behaviour due to the high energy expenditure of prolonged travel, and the increased risk of exposure to unknown threats and predation (Nicholson et al. 1997). To be selectively advantageous, costs must be outweighed by the corresponding benefits, which are most often associated with seasonal resource availability and threat reduction (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2009). These trade-offs can determine whether a population migrates, as well as how far they migrate (Teitelbaum et al. 2015). However, the balance of these trade-offs can change depending on annual fluctuations in weather and resources, or with anthropogenic disturbance (Bradshaw et al. 1998, Fullman et al. 2020, Severson et al. 2021). Obligate migration may be an appropriate behavioral response to consistent, predictable resource cycles, whereas facultative migration may allow for a quicker response to unpredictable resources. As a result, animals are more likely to exhibit facultative migration in areas of unreliable access to resources (Jones et al. 2014, Teitelbaum et al. 2015). The same inconsistency and sudden environmental changes that may benefit facultative migrants would be extremely costly to obligate migrants, who would make the journey regardless of conditions or cost (Devictor et al. 2008). In the face of an increasingly variable environment, flexibility in adaptive behaviours, such as migration, may be key to future survival. It is, therefore, important for conservation purposes to understand if and how individuals might respond to changes in habitat, in order to maintain effective land use and habitat protection plans.

Flexible migration behaviour is a growing topic of discussion among researchers studying caribou (*Rangifer tarandus*) and an important consideration in caribou conservation (Fraser et al. 2018, Weckworth et al. 2018). Certain features of caribou migration vary greatly across Canada, with different populations ranging from fully sedentary, to partially migratory (in which some individuals in a given population consistently migrate), to fully migratory (COSEWIC 2011). Woodland caribou (*R. t. caribou*), particularly within the boreal forest, are generally treated as sedentary in comparison to barren-ground caribou (*R. t. groenlandicus*), a northern subspecies known for extensive, obligate migrations (Theoret et al. 2022). However, some woodland caribou populations have also been observed to be partially or fully migratory in more northern ranges, with potential genetic origins of the behaviour traced back to interbreeding with barren ground lineages (Taylor et al. 2020). While there is marked variation in migration across populations, facultative migration at the level of the individual has not yet been widely explored in woodland caribou.

Within Ontario, woodland caribou are divided into two regional ecotypes based primarily on migratory behaviour. Forest dwelling (FD), or boreal, caribou are often deemed sedentary, with average movement of around 50 km between seasonal ranges (Cumming and Beange 1987, Berger 2004). Forest-tundra (FT) caribou are found further north, and are treated as migratory, with annual migrations over hundreds of kilometres (Abraham and Thompson 1998). Currently, individuals within both ecotypes are often treated as either completely migratory or sedentary; facultative or flexible migration has yet to be explored in either ecotype. It would be valuable to determine whether woodland caribou in Ontario undergo obligate migration, or whether they exhibit facultative migration in response to environmental conditions. Further investigation into the plasticity of their migratory behaviour is important, as it will contribute to a better understanding of habitat use, and may have important consequences for conservation.

Migratory ungulate populations are in decline at a global scale (Kauffman et al. 2021). Migration as a behaviour is itself under threat (Wilcove 2008), as increasing habitat fragmentation and unpredictable resource availability increases the cost of migration and the likelihood of failure to meet energetic needs (Harris et al. 2009). Phenological asynchrony between migration timing and resource waves is also a growing concern, as migratory species are unable to adapt quickly to shifting climates (Mayor et al. 2017, Severson et al. 2021). The vast majority of caribou populations across Canada are also in decline, with most threatened by habitat degradation and range reduction (Vors et al. 2007; Festa-Bianchet et al. 2011). Behavioural plasticity may be necessary to counteract such declines (Lafontaine et al. 2017, Gurarie et al. 2019, Xu et al. 2021). Understanding whether Ontario caribou populations exhibit plasticity in migration behaviour can help to quantify their vulnerability to changes in their environment, and can help to tailor range management plans based on potential changes in range use.

1.2 Migratory syndrome

With migration treated as a flexible behaviour rather than an innate trait, it can become unreliable to label individuals as migratory simply based on seasonal displacement, as that displacement may vary across time and between individuals. This has implications in management decisions which use categories defined by migration, such as the inexact delineation of caribou groupings across Canada (Weckworth et al. 2018, Taylor et al. 2020). Within Ontario, FT and FD ecotypes coincide with the broader Eastern Migratory (DU6) and Boreal (DU4) designatable units (DUs), assigned by COSEWIC (2011). These DUs are assigned based on a combination of differentiating traits, such as morphology, genetic lineages, and locally specific adaptations or behaviours (COSEWIC 2011). These classifications determine conservation status and protection of each ecotype: FT caribou are classified as least concern, while FD caribou are threatened. In Ontario, evidence is somewhat mixed regarding putative genetic or behavioral trait differences between FD and FT ecotypes. The principal distinguishing characteristics are separated calving ranges, and differences in migration strategy (dispersion vs aggregation), at calving season. There is some confusion, however, between migration behaviour and behaviours used to distinguish DUs. While migration distance or frequency are not used for classification, boreal caribou are still treated as fully sedentary, and Eastern migratory caribou as fully migratory.

An alternative and more integrative method of categorization is the concept of a behavioural syndrome. A syndrome consists of a suite of phenotypic traits linked to a single behaviour through co-evolution (Sih et al. 2012). These traits are common across all individuals that fall within the syndrome and can range from morphological, behavioural, or physiological adaptations that directly relate to the behaviour (Dingle 2006). A common behavioural syndrome explored in behavioral ecology categorizes individuals as either ‘bold’ or ‘shy’ phenotypes, where bold individuals show more aggressive and risk-taking behaviours across many ecological contexts, including feeding, mating, and dispersal (Sih et al. 2004). In addition to correlated behaviours, bold individuals may have associated physiological traits, such as increased size or physiological responses, that correlate with a bolder lifestyle (Bonnot et al. 2015). In defining a phenotype or personality based on a series of associated traits, the behavioural syndrome concept provides a quantifiable method of acknowledging the plasticity of behaviour while still categorizing individuals in an ecologically reliable manner (Sih et al. 2012).

Behavioural syndromes also have direct relevance to movement ecology as a means of measuring ecological effects of behaviour on a broader scale (Spiegel et al. 2017). Several studies have examined habitat use and movement of ungulates in the context of personality-driven behaviour. For example, studies on roe deer have found evidence of syndromes in movement such as dispersal and risk-taking; risk-takers have an increased likelihood of dispersal or migration, while risk-averse deer have phenotypes suited for reduced habitat use and exploration (Debeffe et al. 2014, Bonnot et al. 2015). Taking it one step further, migration itself may have its own syndrome. Preliminary research into the topic of migratory syndromes has yet to investigate mammals, but evidence of trait clusters corresponding to migratory phenotypes, including life history traits, body shape and size, and patterns of habitat use, has been observed in birds, fish, and insects (Dingle 2006, Brodersen et al. 2014). One study looking across a more diverse range of taxa demonstrated a method of determining movement-related syndromes based on clusters of movement traits, such as net squared displacement and time in residence, which correspond with different strategies such as migration or nomadism (Abrahms et al. 2017). Migratory syndromes within ungulates in particular is a newer area of interest, and further exploration of this topic could have significant benefits in understanding the movement and ecological interactions of migratory mammals (Sih et al. 2012).

1.3 Research aims

In this study, we investigated the potential for migratory plasticity in two ecotypes (migratory vs sedentary) of woodland caribou and examined the associated suite of environmental correlates of migration. We hypothesized that migration is a flexible space use behaviour in response to inter-annual variation in environmental constraints imposed by resource availability and winter intensity. By comparing migration events and caribou movement to corresponding environmental factors, we aimed to determine how aspects of the environment, such as resources, weather, and habitat disturbance, affect migration and potentially influence whether an individual will migrate in a given year. If the flexible migration hypothesis is correct, then caribou, in either ecotype, will alternate between migratory and sedentary strategies and switches between movement strategies will be associated with changes in the environment. Alternatively, if migration is not flexible, we would expect to see individuals migrate in accordance with the typical behavior of each ecotype; caribou within the northern portion of the range will consistently migrate, and those within the southern portion will remain sedentary across all study years. We also tested whether a suite of movement parameters and habitat selection coefficients provided reliable evidence of a migratory syndrome in Ontario woodland caribou.

2 Methods

2.1 Study area

This study took place across a large portion of northern Ontario, Canada, with some overlap into Manitoba and Quebec, spanning over 450,000 Km^2. Caribou were located primarily within the Hudson Plains ecozone, extending slightly into the Boreal Shield ecozone (Fig. 1; Crins et al., 2009). Landscape varied considerably across the study area, ranging from heavily forested regions to barren tundra. The Hudson Plains ecozone is characterized by cold, short growing seasons, and flat topography. Vegetation in the northern end is primarily coastal wetlands and open tundra, with sparse forest (MNRF 2014). Coniferous forests become more prominent further south, merging into the dense, mixed forest of the Boreal Shield ecozone around the southern edge of James Bay. Human activity is present through the study area primarily in the form of smaller towns (population < 10 000), roadways, railways, and utility corridors, all of which become less frequent farther north (MNRF 2015). Seasonal temperatures, precipitation, and predation pressure also decrease northward.

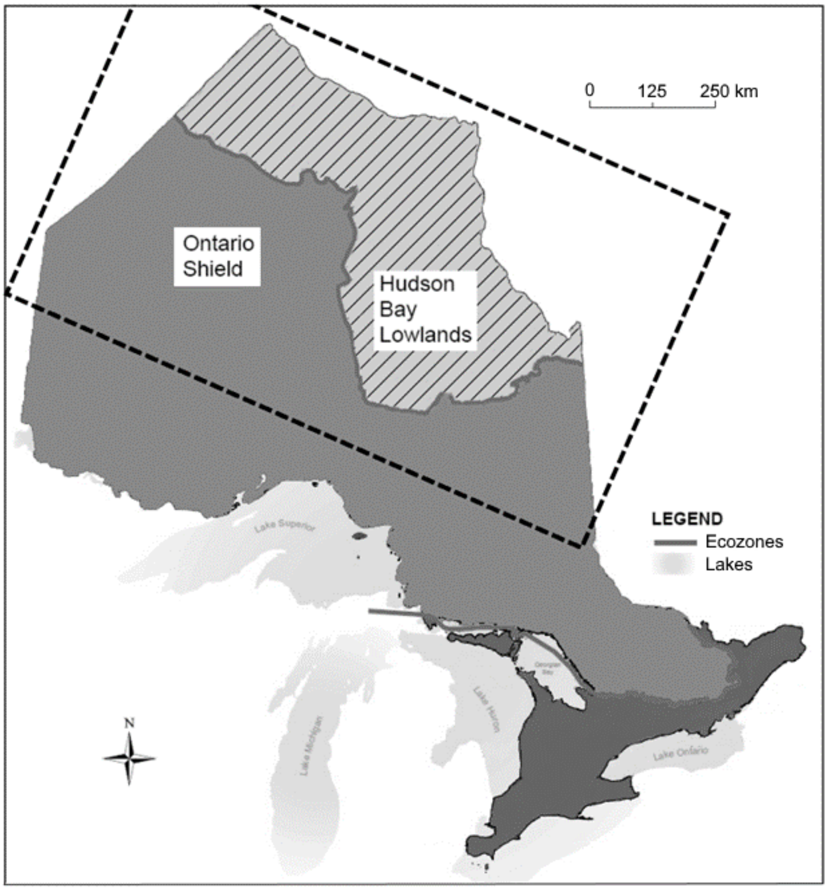

Figure 1. Approximate study area (rectangle) and associated ecozones in Ontario. The study area comprised approximately 450,000 km^2, encompassing a gradient of ecosystems. Caribou were located primarily in the Hudson Plains ecozone, with some overflow into the boreal ecozone. Figure adapted from Crins et al. (2009).

2.2 Study animal

The woodland caribou (*Rangifer tarandus caribou*) is a subspecies of caribou found across Canada (Bergerud 1996). They are a medium-sized member of the deer family found across a diverse range of ecosystems. They are a cold-adapted species, with diet consisting of lichen, grasses, sedges, and woody shrubs in the summer, switching predominantly to lichen in winter (Thompson et al. 2015, Webber et al. 2022). In Ontario, the two regional ecotypes are based primarily on divergent migration and calving behaviour. Forest-tundra (FT) caribou are characterized by long seasonal migrations over thousands of kilometres to aggregate at calving grounds (Bergerud 1996). Females migrate north in the summer, out of the boreal forest, to communal calving grounds in the open tundra and along the coast of Hudson Bay where there is presumably less threat of calf predation. They then return to the boreal forest in winter. Forest-dwelling (FD) caribou differ in behaviour as the females remain in the boreal forest year-round, moving to isolated locations for calving rather than large communal calving grounds. FD caribou are considered sedentary, with more limited seasonal movement (Bergerud et al. 1990). Both ecotypes demonstrate strong site fidelity to individual calving sites, and minimal to no fidelity to winter ranges (Hazell and Taylor 2011).

Movement data from 109 woodland caribou, fitted with GPS telemetry collars, were acquired from three sources (Table A1). We included individuals monitored between 2009-2019 with a minimum of two years of data, in order to identify switching of migration behaviours between years. The final dataset consisted of 88 individuals with two years of GPS data, and 21 with three years of data. Notable outliers in movement (i.e., single step round trips at unreasonable speeds) were eliminated, and data were resampled to GPS fixes at 25-hour intervals to standardize sampling rate across the three datasets.

2.3 Classifying migration

A dominant characteristic of migratory individuals is that they experience two distinct summer and winter range between migrations, and as a result are exposed to two distinct sets of interactions and environments that would not be experienced by a sedentary individual that stays within the same, continuous range year-round (Berger 2004). These differences in land use can provide important insights into the habitat requirements of caribou, and their patterns of interactions with their environment.

Seasonal range separation was used to categorize caribou into movement classes based on ecologically significant differences in habitat use. To calculate seasonal ranges, movement was split into summer (July - August) and winter (January - February) seasons. The months used to calculate seasonal ranges were chosen as the time of year with the least occurrences of accelerated movement, based on monthly distribution of step lengths, where a step refers to the movement between two consecutive GPS fixes. Longer step lengths indicate greater movement within a short amount of time and were therefore presumed to be associated with migration. To determine the points of the year with the least likelihood of migration, we scanned the entire dataset to identify the 10 longest steps for each individual, then determined the months in which the lowest frequency of long steps occurred (Fig. 2). These months were chosen to calculate seasonal ranges as they had the least likelihood of unintentionally capturing movement between seasonal ranges, resulting in less chance of a false negative prediction of migration.

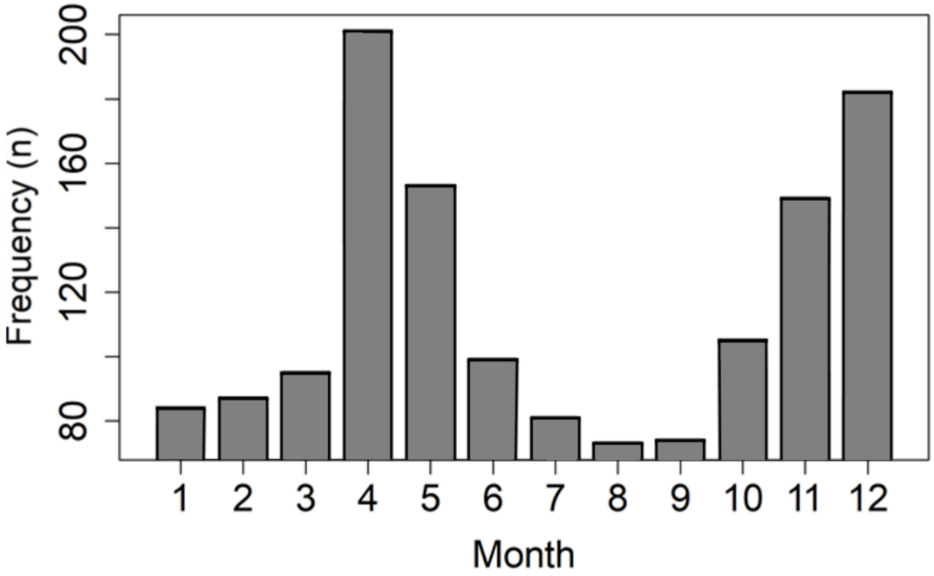

Figure 2. Frequency of max step length per month. Occurrence of the 10 longest steps for each individual was plotted by month to determine the months when individuals were most likely migrating. Resident seasonal range estimates were calculated based on this, using telemetry data from July and August for summer ranges and January and February for winter ranges.

Seasonal ranges were calculated using Brownian bridge estimation. Brownian bridge kernel estimation not only accounts for the placement of fixes, but also estimates the path between fixes based on a simple assumption of Brownian motion over the interval (Horne et al. 2007). This puts greater weight on the area being used and provides an arguably more precise representation of home range use than a simple convex polygon, which often includes unused areas in proximity to used points (Silva et al. 2018). All calculations were performed in R v4.0.3 (R Core Team 2019) using the package AdehabitatHR (v0.4.19).

Many studies around migration in Ontario caribou specifically focus on spring migration, from the winter range to the calving grounds, largely in part due to the importance of calving behaviour in categorization of the local ecotypes (Bergerud et al. 1990, Pond et al. 2016). It is well established that some of the primary driving forces of these spring migrations are predator avoidance and forage availability (Viejou et al. 2018), but it is less established what drives them to leave these low threat areas to return to their wintering ranges. In this study, we chose to focus our investigation on fall migrations in order to contribute to a more rounded understanding of these cycles of movement. Additionally, caribou show extreme site fidelity to their summer ranges, while winter ranges are much more fluid. This made summer ranges a more stable baseline from which to compare fluctuating environmental factors across years.

Based on the seasonal movement between summer and winter ranges, individuals were grouped into four classes: obligate migratory, nomadic, sedentary, or facultative migratory. Migration was defined in this study by movement between disjunct seasonal ranges: no spatial overlap between consecutive summer and winter ranges denoted a migration event. Obligate migratory individuals exhibited consistent, annual migrations, with site fidelity to at least the summer range. Nomadic individuals were more free-ranging, exhibiting movement between seasonal ranges but without site fidelity to any range. Individuals with consistently overlapping seasonal ranges (no migration) were classified as sedentary. Facultative migratory individuals exhibited both strategies, with overlap of consecutive ranges in some years but no overlap other years.

2.4 Environment layers

Several environmental factors were predicted to have an impact on caribou migration, based on their demonstrated effect on forage availability, threat avoidance, and energetic cost of migration (Avgar et al. 2015, McGreer et al. 2015, Fryxell et al. 2020, McNeill et al. 2020). These factors were used to identify how the environment influences patterns of behaviour and impacts the probability and distance of a migration in a given year.

For forage availability we used land cover type and Normalized Difference Vegetation Index (NDVI), which is an estimate of vegetation density and quality based on remotely sensed estimates of visible and near-infrared wavelengths whose ratio is correlated with vegetation green biomass (Pettorelli et al. 2005) . Areas of high NDVI potentially provide increased energy for migration, but also potentially less incentive to migrate in the case of facultative migration (Avgar et al. 2013). High levels of vegetation abundance can also be associated with reduced habitat permeability, which would increase the energetic cost of migration and make prolonged migratory movements less favourable. Weather and climate are often strong drivers of migration as well (le Corre et al. 2017). Heavy snow, for example, increases the energetic cost of movement, making long migrations more costly (Mosser et al. 2014). However, snow cover can also be associated with reduced forage availability (Avgar et al. 2013). This lack of available resources may counterbalance the increased cost of migration and force individuals to relocate, depending on the hierarchy of environmental drivers. In addition to measures of weather and resources, we included several measures of human disturbance to test the impact of human activity on migration. Caribou treat human activity similar to any perceived threat and demonstrate avoidance of industrial development and linear features (Viejou et al. 2018), which can in turn impede migration and limit habitat use (Wilson et al. 2019, Fullman et al. 2020). Human disturbance metrics consisted of populated areas and linear features such as roads, railways, and utility corridors,

All processing of spatial layers was performed in ArcGIS Desktop v10.8.1 (ESRI Inc., 380 New York Street Redlands, CA 92373) and Rstudio. All layers were converted to z-scores to standardize the different scales and units of measure.

2.4.1 Vegetation

NDVI remote sensing data (16-day temporal resolution, 500 m spatial resolution) from the MODIS Terra satellite was acquired from Land Processes Distributed Active Archive Center (LP DAAC) of the NASA Earth Observing System Data and Information System (EOSDIS). Datasets are quality controlled before public release by taking the most reliable pixels from each 16-day window. They are released with a corresponding index of pixel reliability rasters based on the likelihood of obstruction or cloud cover. We adjusted NDVI rasters based on pixel reliability scores to eliminate data errors; vegetation layers were compared against pixel reliability, and pixels flagged as cloud cover were eliminated from the dataset. Mean summer NDVI was averaged spatially across the entire summer range, and temporally for the months of July and August in line with the months used to define the seasonal range in this study.

2.4.2 Snow cover

Snow water equivalent (SWE), defined as the depth (m) of melted water equivalent to snow cover, was used as a measure of snow cover (Vionnet et al. 2021). SWE takes density of snowpack into consideration, so it is useful as both a measure of winter intensity and foraging difficulty for caribou, which must create snow craters to access food (Pedersen et al. 2021). With mass per unit area of snow taken into account, this measurement is linked to both forage availability and energetic costs of travel. SWE raster layers were acquired from the ERA5-land dataset at 0.1 degree (~11 km) spatial resolution. Daily estimates throughout November 1 - December 31 (coinciding with the fall migration season) were averaged across the home range to obtain seasonal estimates of snow cover during migration.

NDVI was also used as a secondary indicator of snow cover and winter intensity in the winter season, as low winter NDVI scores correlates with greater snow cover, especially in open lowland habitats with minimal woody vegetation (Avgar et al. 2013, Thiebault and Young 2020). Mean winter NDVI was estimated using the same methods as summer estimates.

2.4.3 Land cover class

Land cover classes were taken from the Far North Land Cover (FNLC v1.4, spatial resolution = 30 m) dataset provided by the Ministry of Natural Resources and Forestry (MNRF 2014). Classes are estimated based on analysis of remote sensing, geological, and elevation data from 2006-2011. Following Avgar et al.’s (2013) methodology, the original 24 classes in the dataset were aggregated to form seven broader classes based on dominant vegetation, each with distinct benefits and energetic consequences for caribou (See Table 1). This allowed for more parsimonious models with fewer terms, as well as it reduced noise from land cover features that were not relevant to this analysis, such as differentiating between types of wetlands. Final classes consisted of water (FNLC 1-2), sparse vegetation (FNLC 3-5, 7, 15), lowland (FNLC 6, 8-14), deciduous (FNLC 16), mixed (FNLC 17), coniferous (FNLC 18), and disturbed (FNLC 19-24).

Table 1. Landcover class breakdown and description. Classes from the MNRF Far North database were combined based on dominant vegetation. Descriptions are based on Far North Land Cover (FNLC) classification descriptions (MNFR 2014).

Class	FNLC	Description
Water	1,2	Clear or turbid water. Sparse aquatic vegetation, no tree or shrub cover.
Sparse	3-5,7,15	Unvegetated coastal mudflats, marshes, and sparsely treed inland. Tree and shrub cover is approximately <25%, primary food sources caribou consist of sedges, grasses, and lichen.
Lowland	6,8-14	Treed marsh, swamp, fen and bog. Dense shrub cover of ≤ 25%, sparse tall tree cover around or under 10%. Food sources are predominantly lichen, moss, and ericaceous or low shrub.
Deciduous	16	Dense deciduous tree cover (>60% closure), predominantly consisting of poplar and birch.
Mixed	17	Dense, tall tree cover (>60% closure). Mixture of deciduous and coniferous trees, such as jack pine, spruce, birch, and poplar.
Coniferous	18	Dense coniferous tree cover (>60% closure). Predominantly jack pine and spruce. Dense, old growth, coniferous forests often facilitate lichen growth on trees, representing an important food source for caribou in winter (Avgar et al. 2013).
Disturbed	19-24	Land that has been disturbed at some point over the past 20 years, consisting of low or sparse tree cover, or was currently disturbed at the time of data collection. Including sparse woody, regenerating forest, bedrock, mine tailings, and towns/anthropogenic infrastructure.

2.4.4 Human disturbance

Spatial layers for roadways, railways, utility corridors, and populated areas were obtained from the Ontario Geospatial Data Exchange (OGDE). In order to measure broad-scale patterns of movement in relation to these features, we converted the spatial layers from presence/absence metrics to a proximity-based metric. Vector layers were converted to raster layers at a 500-m resolution in ArcGIS, with each grid pixel containing values representing proximity to the populated area or linear feature. This allowed us to test at a broad scale how distance from human activity correlates with migratory behaviour. Measurements were averaged across the entire home range of each individual to obtain yearly averages of proximity to human infrastructure.

2.5 Statistical analysis

Following the classification of migratory individuals, linear mixed models were used to investigate the effect of the environment on the probability and distance of migration. The focus of the analysis was on fall migration away from the breeding grounds to a wintering range. Since caribou show strong site fidelity to summer calving ranges, often returning within several kilometres (Berglund et al. 2014), summer ranges were treated as the baseline range, with the analyses examining how factors within their summer range might drive migration to an alternate range in winter. Specifically, we looked at how location (represented by latitude, longitude, and proximity to coastline), vegetation, winter intensity, and human disturbance within the summer range affected the probability of migration in a given year. Then, in the event of a migration, we looked at how those same factors correlated with distance of migration.

In tandem with the migration analysis, we also tested for a migratory syndrome by pulling habitat selection coefficients and migration associated movement metrics, and then running a cluster analysis to identify patterns of commonly associated traits. To determine whether these trait clusters were also associated with migration, we cross referenced the cluster with our predetermined movement classes with an R x C contingency table and ran a chi-square test of independence to test for significant overlap between the two classification schemes. All statistical analyses were performed in Rstudio.

2.5.1 Probability of migration

A generalized linear mixed model (GLMM, binomial family, logit link) was performed (package lme4 v1.1-29) to estimate the effect of environmental conditions on the likelihood of fall migration within a given year. All individuals were included in this analysis, each with two to three migration events per individual, for a total of n = 241 observations. Range estimates of vegetation, snow cover, and human disturbance metrics previously outlined were included initially in the model, along with spatial measures of latitude, longitude, and distance from the Hudson Bay coastline. Individual was included as a random effect to account for repeated sampling across individual caribou and for imbalance in sampling among individuals (Gillies et al. 2006). Significance of random effect was tested with a likelihood-ratio test (LRT). Collinearity was tested by comparing pairwise correlations for all variables. Based on the methodology of Dormann et al. (2013), one variable of each pair exceeding a threshold of $R^2 >= 0.6$ were excluded from the analysis. The decision of which variable per collinear pair to exclude was made based on AIC comparison, which eliminated two collinear variables from the original model. Model parsimony was tested using AIC. The model was also tested for overdispersion and normality of random effects (Zuur et al. 2010, Denomme-Brown et al 2020); all assumptions were met by the final model.

2.5.2 Distance of migration

To estimate how environmental factors affect variability in migration distance, we ran a linear mixed effects model. We cut the dataset to only include migratory years ($n = 205$); Individuals which were identified as migratory, as well as the migratory years of nomadic and facultative migratory individuals, were combined for the analysis. Migration distance was estimated as the linear distance between centroids of summer and winter ranges. Distance was compared in the model against the same environmental factors as the previous analysis, with the most parsimonious model chosen based on AIC. Individual identity was maintained as a random effect to account for repeated sampling. The model did not pass the assumption of homogeneity of variance of the residuals (Breusch-Pagan test, $BP(8) = 50.57$, $p < 0.001$). A linear mixed effects model was still used as they have shown robustness to violated assumptions, and while heteroscedasticity affects the precision of estimated errors, it should not bias the model (Schielzeth et al 2020). That being said, caution should be taken in evaluating the model estimates. Assumptions of linearity, independence, absence of outliers, and normality of residuals were all met by the final model.

2.5.3 Migratory syndrome analysis

Following our analysis on the environmental determinants of probability and distance of migration, we also tested the potential for a migratory syndrome in caribou by investigating for naturally occurring clusters of migration-associated traits across the population. For this analysis, we partitioned the dataset to include just the first two years of GPS data per individual, in order to balance the dataset for comparison between individuals (n = 109).

Step selection is a form of resource selection analysis performed at the level of a step. It uses conditional logistic regression to compare the conditions of used steps compared to those of a randomly generated set of available steps within the area. This kind of test is used to identify what variables in the nearby environment an individual is responding to, and what types of habitat are being used most frequently. An integrated step selection analysis (iSSA) is a form of step-selection function that reduces bias by taking individual movement patterns into account when generating random available steps. Rather than sampling from the observed step lengths and turn angles, available steps are generated from parametric distributions that are fitted to step length (gamma distribution) and turn angle (Von Mises distribution) to more closely imitate natural behaviour (Avgar et al. 2016). We ran an iSSA to analyze selection for vegetation, snow cover, and land cover type at the level of the individual. The model was tested for and met assumptions of no collinearity and absence of extreme outliers. Significant step selection coefficients (representing attraction to or repulsion from various landscape features) were extracted for a subsequent cluster analysis.

In addition to selection coefficients, several movement metrics were extracted from the data using the R package AMT (v0.1.3). Mean step length, maximum step length, and mean turn angle were calculated for each individual for use in the cluster analysis. Larger step lengths indicate elevated movement rates and are likely associated with migration. Turn angle is associated with directionality: a measure of whether a step is aligned in a similar direction as the previous step, or if movement is more random. Therefore, patterns of both step length and turn angle can be used to identify a migratory individual; migration would be associated with patterns of higher mean or max step length, and lower mean turn angle (Abrahms et al. 2017).

A principal component analysis (PCA) was performed with the movement metrics and selection coefficients, to condense the data. The principal components (PC) were then used in a Hierarchical Cluster on Principal Components (HCPC) analysis. This involves a cluster analysis in which a suite of variables is first simplified into principal components, and then the dataset (n = 109) is divided into clusters of similar sets of variables using a combination of hierarchical and partitioning cluster methods (Lê et al. 2008). Nested clusters are divided based on a hierarchical tree; recommended number of clusters is estimated statistically based on growth of within-group inertia.

The clusters defined in this analysis were then compared to the movement classes predetermined in this study, to see if all individuals within a movement class also share similar movement and selection traits). A chi-squared test was used to identify significant overlap or common trends between movement classes and statistically assigned clusters.

3 Results

3.1 Movement classes

Of the 109 caribou sampled in the James Bay basin, 74 were categorized as obligate migratory, 16 as facultative migratory, 14 as nomadic, and 5 as sedentary (Fig. 3). Sedentary individuals were found in two distinct locations: the southern end of the James Bay coastline and the most inland portion of our study area, within the boreal shield. Migratory and nomadic individuals were spread out throughout the study area (Fig. 4).

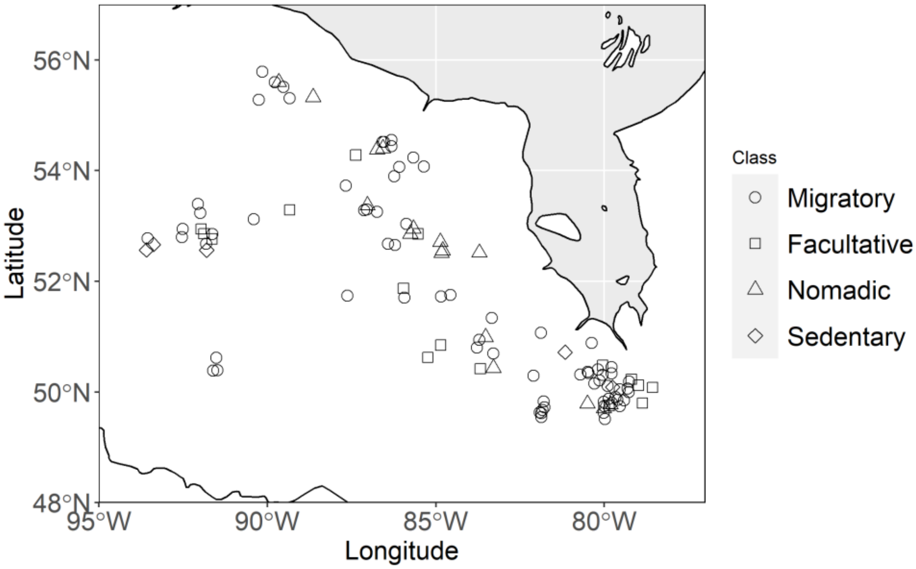

Figure 3. Spatial distribution of caribou movement classes. Points represent the centroid of the winter range from the first year of observation of each individual. Migratory and nomadic caribou were found spread across the study area, while sedentary individuals were clustered in two locations.

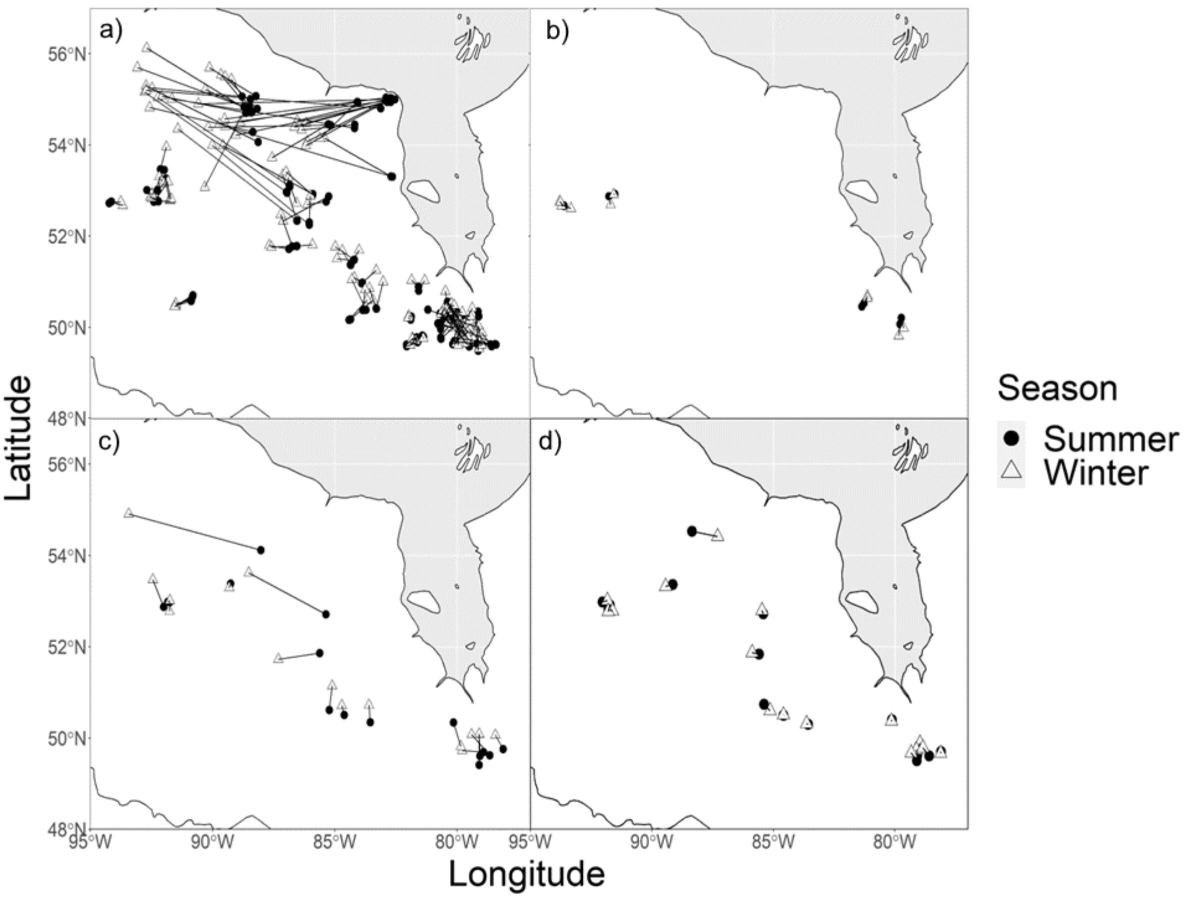

Figure 4. Range separation for individual caribou from the fully migratory (n = 74) (a), sedentary (n = 5) (b), and facultative migratory (n = 16) (split into migration years (c) and sedentary years (d)) classes. Lines represent the linear distance between the centroids of a summer range and the consecutive winter range. For migratory individuals, this distance correlates with migration distance.

Annual variability in migration strategy was found within individual migrants across the entire study site: 15% of observed individuals exhibited facultative migration, switching between migratory and sedentary behaviour across years. Individuals in the north showed the greatest variation in annual movement; the longest migration distance by a facultative individual was 451.1 km in a migratory year, following a sedentary year where the distance between seasonal ranges was only 38.1 km. Within the forest-dwelling region, there was much less drastic difference in travel distance for facultative individuals between migratory and sedentary years than that found in the northern (FT) individuals. Migration distance for individuals below 52° latitude never exceeded 150 km, with an average distance of 46.3 km.

The majority of facultative migratory individuals tended to demonstrate the same movement behaviour in a given year. In 2009, 85% of observed facultative individuals demonstrated sedentary behaviour, while in 2010, 88% migrated. This pattern became less pronounced in later years, as fewer (< 5) facultative individuals were recorded, and those only occurred in the far south of the study range.

3.2 Environmental correlates of migration

Migration frequency was found to be most strongly correlated with weather and resource fluctuation, with GLMM analysis (Table 2) demonstrating that the probability of migration was positively associated with increase in snow cover in the fall travel period ($\beta = 3.30 \pm 0.92$, $p < 0.001$) and summer NDVI ($\beta = 2.54 \pm 1.18$, $p = 0.03$). Migration showed no correlation with location (latitude, longitude, proximity to Hudson Bay coastline) or proximity to human disturbance.

This analysis was also repeated using only the first two years of movement data for each individual, in order to test the analysis with a reduced imbalance of observations between individuals. Consequently, to evaluate whether annual differences in the dataset influence which patterns are most prominent, we performed a pairwise comparison of probability analyses for each pair of years, repeating the GLMM three times while varying which years were chosen (1st and 2nd, 2nd and 3rd, 1st and 3rd) from the 21 caribou with three years of data (Appendix: Table A2). This analysis showed that interannual variation can alter which correlates of migration are most pronounced, however NDVI and snow cover were both maintained as significant predictors of migration behaviour across several of the analyses (see Appendix: Tables A3-5).

Similar to the probability analysis, migration distance was also found to be correlated with fall snow cover ($\beta = 40.23 \pm 5.39$, $p < 0.001$), and showed no correlation with proximity to roads or utility corridors ($p > 0.1$; Table 3). Additionally, spatial trends were seen in migration distance. Distance was correlated positively with latitude ($\beta = 123.1 \pm 16.91$, $p < 0.001$; Fig. 5), as well as longitude ($\beta = 72.06 \pm 18.78$, $p < 0.001$), essentially increasing northwest in the range. NDVI also showed no significant correlation with migration distance. Conditional R-squared, calculated using MuMIn package (v.1.46.0) based on the methods in Nakagawa et al. (2017), was found to be 0.75 for the model. A pairwise comparison of 2-year analyses was also performed with the migration distance analysis, however no change in correlates of migration distance was seen when analyzed across different years (see Appendix: Tables A6-9).

Table 2. Summary results of statistical analysis for probability of migration of Ontario woodland caribou in response to interannual fluctuations in the environment. Probability was tested with a generalized linear mixed model (binomial family, logit link). Environmental factors (vegetation, snow cover, human disturbance) were included as fixed effects, individual was included as a random effect to account for repeated sampling. Bold terms represent significance ($p < 0.05$). Significance of random effect was tested with LRT.

Model	Behaviour (1/0) ~ NDVI (summer) + Snow cover + Distance from Hudson Bay + Distance from roads + Latitude + Snow cover: Latitude + Individual (random)				
	Variable (type)	β ± SE	Z-value	p-value	X^2
	$\text{NDVI}_{\text{summer}}$ (Fixed)	**2.54 ± 1.18**	**2.16**	**0.03**	**-**
	Snow cover (Fixed)	**3.30 ± 0.92**	**3.59**	**0.0003**	**-**
	Distance from Hudson Bay (Fixed)	-0.13 ± 0.90	-0.14	0.89	-
	Distance from roads (Fixed)	1.43 ± 1.42	1.01	0.31	-
	Latitude (Fixed)	2.58 ± 1.56	1.65	0.10	-
	Snow cover: Latitude (Interaction term)	0.61 ± 0.90	0.68	0.49	-
	Individual (Random)	-	-	**1.79e-5**	**32.74**

Table 3. Summary of results from statistical analysis of migration distance of Ontario woodland caribou relative to interannual changes in environment (vegetation, snow cover, human disturbance). A linear mixed model was used, with individual as a random effect to account for repeated sampling of caribou. Bold terms represent significance ($p < 0.05$). Significance of random effect was tested with LRT.

Model	Distance ~ NDVI$_{(summer)}$ + Snow cover + Distance from Hudson bay + Distance from roads + Distance from utility corridors + Latitude + Longitude + Snow cover:Latitude + Individual (random)					
	Variable (type)	β ± SE	Z-value	df	p-value	X2
	NDVI$_{(summer)}$ (fixed)	-7.27 ± 8.12	-0.89	93	0.37	-
	Snow cover (fixed)	**40.23 ± 5.39**	**9.90**	**93**	**0.0003**	**-**
	Distance from Hudson bay (fixed)	25.78 ± 14.49	1.77	93	0.07	-
	Distance from roads (fixed)	9.84 ± 7.54	1.30	93	0.19	-
	Distance from utility corridors (fixed)	19.30 ± 8.81	1.06	93	0.29	-
	Latitude (fixed)	**123.1 ± 16.91**	**7.28**	**93**	**0.00**	**-**
	Longitude (fixed)	**72.06 ± 18.78**	**3.83**	**93**	**0.0002**	**-**
	Snow cover:Latitude (interaction)	**61.73 ± 6.23**	**9.90**	**93**	**0.00**	**-**
	Individual (random)	-	-	**6**	**0.00**	**237.49**

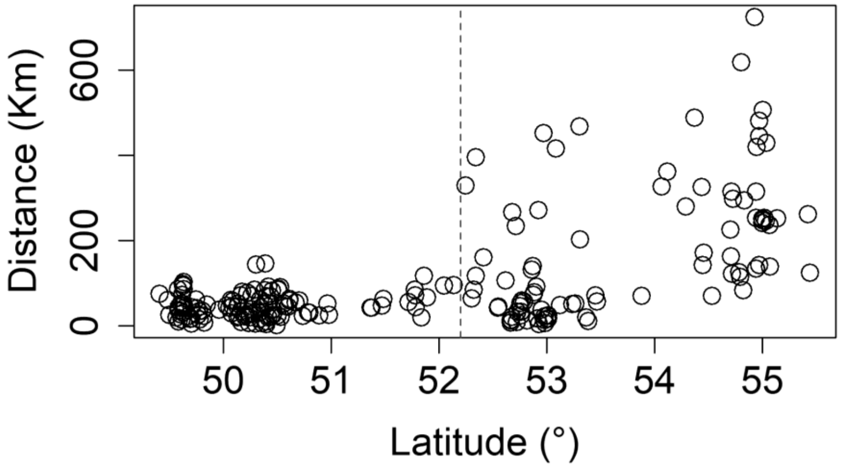

Figure 5. Distance (km) between seasonal ranges in relation to latitude (°). Dashed line represents the latitude (52.2° N) with the greatest change in maximum distance (per latitude). Individuals north of that latitude demonstrate significantly greater variance in distance than those to the south.

3.3 Migratory syndrome

From the step selection analysis, we found significant variation in selection for environmental variables among individuals. Most individuals showed no preference for or against water, deciduous, or mixed forest land cover classes ($p > 0.5$), while positive selection was observed for sparse (mean selection coefficient: 1.53 ± 0.70), lowland (1.15 ± 0.82), coniferous (1.34 ± 0.82), and disturbed (1.19 ± 1.0) classes. Individuals showed weak positive selection for vegetation, with mean selection for NDVI of 1.14e-04 ± 1.6e-04. Selection for snow cover showed the greatest variation in selection, with some individuals showing no significant selection for or against snow, others demonstrating avoidance towards increased snow, while others positively selected for it (mean selection coefficient: 39.68 ± 246.41).

Selection coefficients were combined with movements metrics (mean step length, maximum step length, and mean turn angle) for the PCA. Three of the nine principal components were retained based on kaiser criterion (only PCs with eigenvalues >1 are retained), accounting for 73.7% of the variation in the data. Contributions by each variable are broken down for each component in Table 4, with PC-1 representing selection for landcover variables (sparse, lowland, coniferous, or disturbed), PC-2 representing movement metrics (mean step length, maximum step length, and mean turn angle), and PC-3 comprised of a combination of selection for NDVI and snow cover (Fig. 6).

The HCPC analysis partitioned the data into three clusters based on inertial gain (Fig. 7). Cluster 1 (C-1) represented individuals with high mean and maximum step length, low mean turn angle, and low selection for landcover. Cluster 2 (C-2) contained individuals with low mean selection for landcover, low step length, and higher mean turn angle. Finally, individuals within cluster 3 (C-3) demonstrated high selection for landcover, higher mean turn angle, and wider variance in step length. All clusters showed extremely variable selection for both NDVI snow cover. The analysis was also run at four clusters in order to better compare to the four movement classes, but further breakdown of clusters past three provided no meaningful difference in trait clustering, spatial distribution, or comparison to classes.

Table 4. Breakdown of principal components (PC). This table shows the percent of variance in the overall data, and the percent of each variable that is accounted for within each PC. Bold numbers represent highest percent contribution of each variable. Approximately 73.7% of the variance in the data is explained by the first three PCs in the model.

	Principal Component		
Loadings	1	2	3
Movement metrics			
Mean step length	8.18	**28.29**	0.31
Max step length	1.58	**25.76**	1.42
Mean turn angle	7.35	**28.32**	0.65
Selection metrics			
NDVI	3.21	0.12	**39.16**
Snow cover	1.71	0.01	**57.75**
Sparse landcover	**19.57**	3.41	0.30
Lowland landcover	**22.27**	6.35	0.11
Coniferous landcover	**20.66**	4.65	0.12
Disturbed landcover	**15.47**	3.09	0.18
% Variance explained	38.34	23.74	11.63

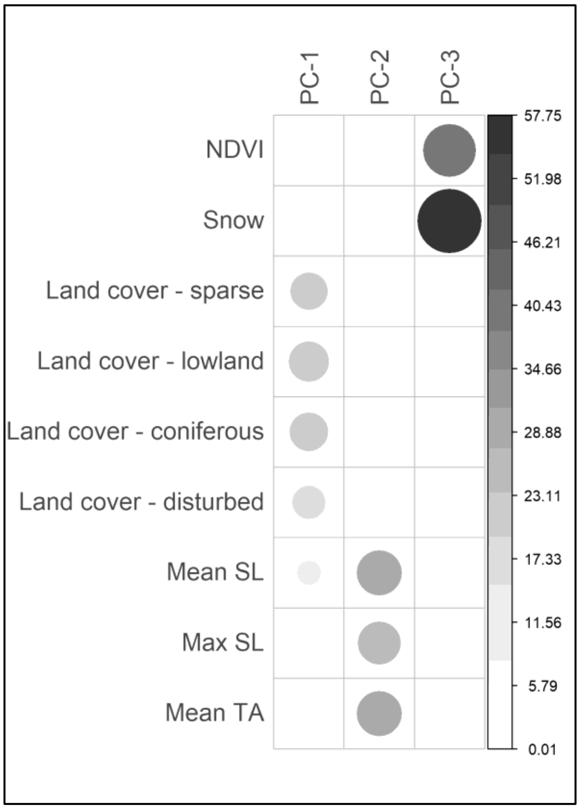

Figure 6. Correlation matrix depicting the contribution of each variable to the three principal components (PC). PC-1 axis predominantly demonstrates selection for landcover; PC-2 represents directionality (mean turn angle, TA), and mean and max step length (SL); and PC-3 represents a combination of selection for NDVI and avoidance of snow cover.

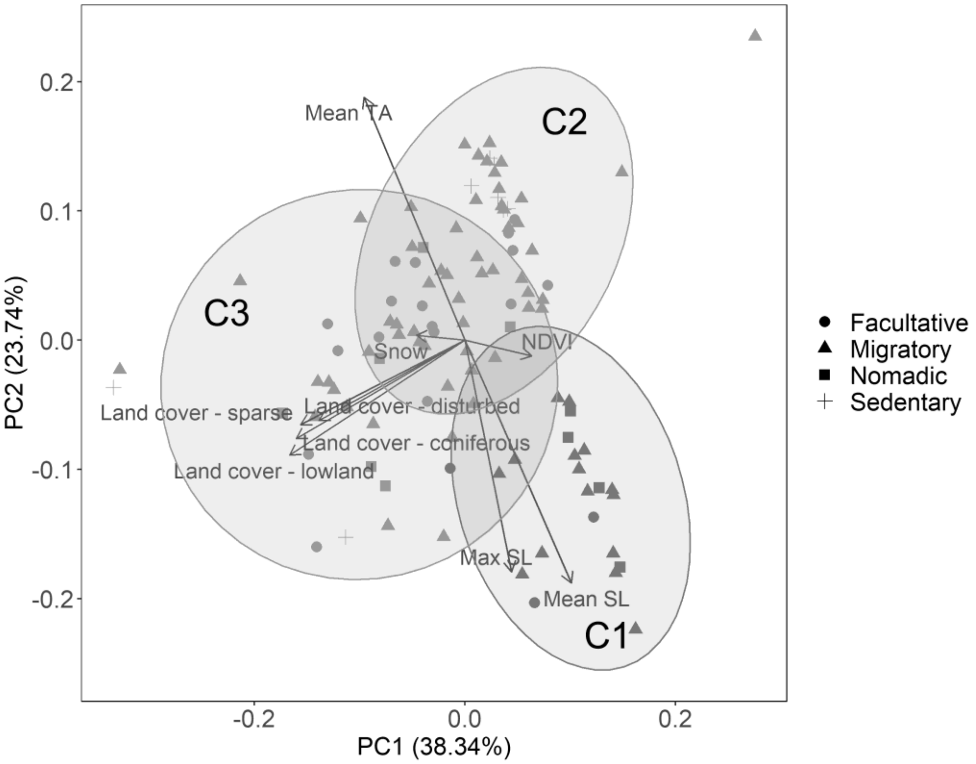

Figure 7. Cluster breakdown of HCPC analysis, plotted against the primary and secondary principal components. Three clusters of correlated migration traits were found in the data: cluster 1 represents high step lengths, low mean turn angle and low selection for land cover, cluster 2 represents low step lengths, high turn angle and low selection for land cover, and cluster 3 represents high selection for landcover, higher turn angle, and variable step lengths. Movement classes, as assigned in this study, were evenly divided across all three clusters, no overlapping pattern was found between movement classes and data clusters.

Further investigation into the composition of each cluster showed that there was little or no overlap between clusters and the movement classes developed in this analysis; a Pearson's chi-squared test on a contingency table confirmed that individuals of each independently assessed migratory class were evenly divided up among the clusters ($X^2 = 8.24$, df = 6, $p > 0.1$, Table 5). However, we did find spatial trends in the clusters, with similar distribution to the designated ecotypes (Fig. 8). C-1 was predominantly found in the north of the study range, coinciding with the FT ecotype, whereas C-2 and C-3 clusters were spread throughout the FD range.

Table 5. **Contingency table depicting frequency distribution of caribou across movement classes and trait-based clusters**. No statistically significant association was seen between migration behaviour and clustered movement and selection traits.

	Cluster		
Movement class	1	2	3
Migratory (obligate)	15	36	23
Facultative	1	9	6
Nomadic	5	3	6
Sedentary	0	2	3

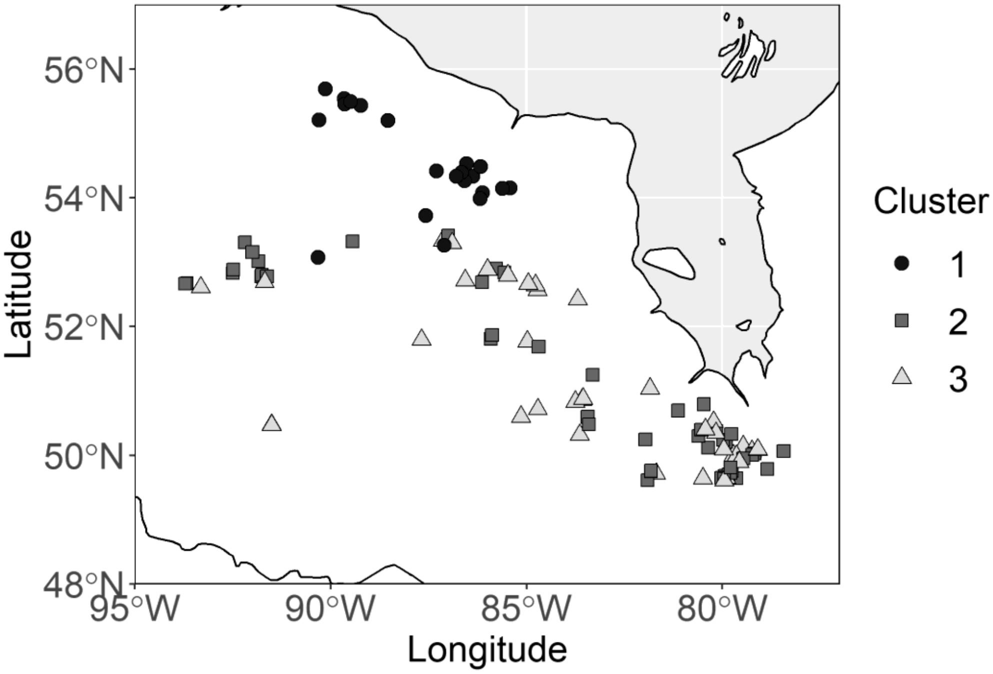

Figure 8. Spatial distribution of HCPC clusters. Caribou in cluster 1 were located at the north end of the study range, coinciding with the established range of the FT ecotype. Clusters 2 and 3 were both distributed throughout the southern end of range, showing minimal overlap with Cluster 1.

4 Discussion

4.1 Facultative migration in Ontario caribou

Migratory plasticity holds ecological significance, reflecting both resilience to temporary environmental change, and nuanced habitat selectivity. Migration is often hypothesized to provide a long term, evolutionarily adaptive solution to cyclical patterns of resource scarcity or predation threat, but it is a costly behaviour and susceptible to severe consequences in the face of rapid environmental change (Avgar et al. 2014, White et al. 2014). Many migratory species are declining as habitat fragmentation can impact key migratory routes, or as changes in climate drive phenological asynchrony (Berger 2004, Mayor et al. 2017). As a result, behavioural plasticity is increasingly viewed as an important ingredient for persistence (Mayor et al. 2017, Severson et al. 2021, Xu et al. 2021).

Our results support the hypothesis that migration in caribou can be a flexible response to changing stimuli for a small fraction of the population. Several other recent studies have looked to better understand flexibility in migratory ungulates, with similar results to our own (Eggeman et al. 2016, Berg et al. 2019, Xu et al. 2021). Instances of facultative migration and general migratory plasticity in response to environmental, social, and other cues have been found in several species of ungulates, including elk (Eggeman et al. 2016), mule deer (van de Kerk et al. 2021), and other populations of caribou (Joly et al. 2021, Theoret et al. 2022). These studies demonstrated flexibility in response to a variety of specific pressures. Elk, for example, exhibited facultative migration that was primarily determined by age and population abundance (Eggeman et al. 2016). Another study connected likelihood of bison migration to a combination of factors including population density, genetic predisposition, and climate variation (Bruggeman et al. 2008). Our results complement these findings with similar patterns of migration in response to climate variation (i.e. snow), while additionally revealing a population-wide pattern of decision-making that has not been thoroughly documented.

Our research suggests population-wide patterns in broad scale movement among facultative migratory individuals. Many facultative individuals undertook the same behavioural strategies across several years: the majority did not migrate in 2009, and then migrated in 2010 and 2012. Facultative migration at a population level has not been thoroughly studied, and to our knowledge, this is the first record of such recurrent patterns within woodland caribou. These results support the theory that flexible migration may be in part driven by range-wide, extrinsic factors such as climate variation; individuals capable of facultative migration are responding to the same widespread environmental stimuli (Bruggeman et al. 2008). Years in which the majority of facultative individuals undertook migration coincided with greater mean annual snow cover. Strong conclusions cannot be drawn due to limitations on sample size of facultative individuals, but the pattern suggests that these individuals chose to migrate each year in response to external stimuli, including snow cover or winter intensity. This pattern is particularly interesting within FD caribou, as they do not migrate en masse, but rather disperse during calving season (Bergerud et al. 1990). This suggests that the common decision to migrate is not a socially-driven consensus, but rather a shared trait across individual caribou in response to a common environmental stimulus.

4.2 Environmental drivers

Understanding the driving forces behind migration provides us with important information on the needs of an individual or population. From a conservation perspective, it can help to identify key habitat and predict consequences of future disturbances. In the case of migration, the driving force behind movement revolves around energetic and other fitness trade-offs (Avgar et al. 2014, Mosser et al. 2014). The fitness benefits of migration, such as seasonal resource availability or threat avoidance, must outweigh the high cost of movement (White et al. 2014).

Snow cover had one of the strongest effects on migration, despite increased snow cover corresponding to greater energetic cost of travel (Mosser et al. 2014). Similar trends of increased migration with greater snow cover or winter intensity have previously been seen in roe deer and mule deer, both species of which food sources are similarly limited by snow (Nicholson et al. 1997, Cagnacci et al. 2011).

The effect of vegetation on migration is not as clear. Estimates of NDVI within the summer range of caribou appeared to influence the probability of a migration occurring in a given year, but had no effect on the distance of a given migration. Greater NDVI was associated with a greater probability of migration, potentially indicating that caribou will migrate on the condition of adequate resource gain prior to departure. However, once the migration has begun, other factors must influence when and where they will stop.

Linear features and human disturbance showed little correlation with probability and distance of migration at this scale of analysis. Anthropogenic features have been seen to influence caribou space use behavior in several ways: at a finer scale of movement, linear features alter habitat permeability, and areas of high traffic and activity are perceived as threats and avoided (Beyer et al. 2016, Prokopenko et al. 2017a). It is possible that this pattern is not seen at a broader scale of movement. Additionally, effects of predation are intertwined with human influence: linear features that impede prey movement can facilitate predators (Dickie et al. 2020), and both are sources of mortality in their own right. It is difficult to ascertain the full impact of human disturbance without information such as predator presence and predation rates, however this information is limited within the far north of Ontario. It would be worthwhile for future research to address this information gap, potentially at a smaller scale of analysis.

4.3 Categorizing migration

Variability in both frequency and intensity of migration in caribou was found across our entire study range, even at the north end within the established range of the forest-tundra ecotype (Fig. 3). Several northern individuals demonstrated divergence from the “classic” FT caribou definition of long migrations up to thousands of kilometres to the Hudson Bay coast (Bergerud 1996). While some individuals migrated over 500 km to calve right on the coast, others travelled less than half that distance and settled further inland on the Hudson plains. Individuals in the southern end of our study demonstrated far shorter migration distances in comparison to their northern counterparts.

With the limited scale of migration in the more southern caribou, it would be tempting to discount their migrations as ecologically similar to sedentary behaviour. FD caribou in general are often treated as sedentary, including in Provincial and COSEWIC documentation (COSEWIC 2011, Festa-Bianchet et al. 2011, COSEWIC 2017). Our results suggest that this may be an oversimplification, ignoring the ecological and energetic consequences that still exist with FD caribou. Defining a population as sedentary can be misleading, as many FD caribou consistently migrate more than 100 km in a year.

Moreover, attempts to categorize movement as either sedentary or migratory befall the same difficulties as identifying a long distance versus short distance migration; clear and consistent delineation between the two is rarely found in a natural setting (Berger 2004). Even when a distinction is present, it is then important to consider whether the categorization serves a purpose, particularly when it may affect policy. In the case of migration, a principal characteristic stands to be the cyclical use of two distinct, seasonal ranges. From an ecological standpoint, this characteristic mirrors a clear distinction in habitat use and environment-facilitated interactions between migratory and non migratory individuals. Such a distinction is not as clear in attempts to delineate short versus long migratory individuals. FD caribou ranges separated by only several kilometres can possess distinct sets of environmental stimulus, threats, and cues, and important information can still be gleaned from these short migrations the same as it would for more pronounced migrations (Berger 2004, Hazell and Taylor 2011). Research on fine scale habitat use of boreal caribou have highlighted differences in predation, calf mortality, and resource availability that is reflected by inter-individual variation in movement patterns (Avgar et al. 2013, 2015, Viejou et al. 2018, McNeill et al. 2020). Patterns of avoidance or use of roads and corridors has also been documented, providing useful insight into movement patterns which can be used to produce stronger predictive models and inform conservation decisions (Thurfjell et al. 2014, Prokopenko et al. 2017a, Fullman et al. 2020). Improved understanding of the factors contributing to migratory flexibility, even within small scale movements, can provide important clues for understanding the adaptive basis for habitat selection and response to environmental changes.

Spatial variation in behaviour was not a consistent delineator between ecotypes either. Distance, but not probability, of migration was positively correlated with increasing latitude. Distance of migration exhibited spatial patterns similar to what was expected based on the ecotypes; southern individuals demonstrated short migrations corresponding with FT ecotype, while individuals further north exhibited long migrations as expected from the FD ecotype. However, while overlap between ecotype ranges sits approximately around latitude 53-55◦ N, the greatest difference in average distance per latitude occurred closer to latitude 52.2 ◦ N (Fig. 5). Below latitude 52.2◦ N, distance between ranges never exceeded 150 km as expected for sedentary FD caribou. Maximum distance per latitude then jumped approximately 120 km around 52.2◦ N, still within the known FD range. Above that, individuals demonstrated much greater variance in migration distance; maximum distance increased almost linearly with latitude, while minimum distance remained quite low (Fig. 5).

Distinct behavioural differences between the ecotypes break down further in the area of overlap between the two ecotype ranges. Within the area of range overlap, caribou of both ecotypes demonstrate similar intermediate migration distances, and equal potential for facultative migration. Similar intermediate behaviour was observed in a previous study on a small subset of caribou located near the boundary between ecotypes (Hazell and Taylor 2011). Caribou in this study demonstrated variation in both migration distance and home range size, averaging farther migrations than individuals further south but shorter than more northern individuals. This variation suggests either that both migration strategies are successful within this range, or possibly that both ecotypes are able to adjust their movement strategy enough to succeed in a less-than-ideal habitat at the edges of their known range. As potential future range shifts might be expected to further increase the overlap between caribou ecotypes, it will be important to understand whether each ecotype will be equally capable of adjustment to the new conditions.

Historical trends in range shifts show the FT caribou range expanding east down the coastline, while the southern edge of FD caribou range has been receding for decades (Schaefer 2003, Newton et al. 2015). Boreal caribou in particular are experiencing greater rates of habitat loss and range reduction in the southern edge of their range (Vors et al. 2007, Wilson et al. 2019). Anthropogenic activity such as deforestation and industrial expansion have been shown to negatively impact population viability of herds (Fryxell et al. 2020). Northward range shift and merging with FT populations may be one way to compensate for the southern range recession, but it is not known whether they will be able to adapt to northern conditions and compete with FT counterparts. Within our study, caribou in the FT range demonstrated variability in behaviour, which bodes well for their ability to respond to future changes in their environment, such as altered vegetation and growing seasons, or increased human disturbance (Gurarie et al. 2019, Joly et al. 2021, Neilson et al. 2022). Southern FD individuals, on the other hand, demonstrated a potential behavioural limit; migration distance, while still variable, reached a maximum of 150km. It is important to understand whether this limit is intrinsic or extrinsically based, in order to predict the population's resilience. If consistently shorter migrations are an adaptive response to ample resources and optimal location, there may be no impediment for southern caribou to adapt to a northern environment. However, if migration has an intrinsic limit, genetic or otherwise, southern populations may be incapable of northern range expansion, and therefore more vulnerable to southern anthropogenic disturbances.

The flexible nature of migration makes it imprecise to categorize individuals as strictly migratory or sedentary. While past studies have found preliminary evidence of a behavioural syndrome linked to migratory phenotypes in ungulates (Dingle 2006, Debeffe et al. 2014), our cluster analysis did not find an overlying pattern within the movement or small-scale selection tendencies of woodland caribou associated with migration. It is possible that this is a result of the plasticity in migration; if migration is used as a flexible solution to short-term changes, long-term adaptations that are evolutionarily associated to migration may be muted, or even missing. The cluster analysis did, however, find similarities in spatial distribution between the clusters and the two established ecotypes. The northern cluster (C-1, characterized by long steps, avoidance of snow, and low selection for any given land cover class) coincided strongly with the FT ecotype range, with almost complete spatial separation between C-1 and C-2/C-3 (Fig 7). This provides additional support for behavioural distinction of ecotypes, however this distinction should not be based on sedentary vs. migratory behaviour, as neither the clusters or ecotypes matched the divisions of migration behaviour.

4.4 Limitations

While this analysis established the presence of facultative caribou within Ontario populations, a similar analysis on individuals with more than two years of data would greatly improve the ability to identify facultative individuals, possibly revealing more variation than was captured here. Additionally, a longer observation period would also contribute more confidence to patterns of environmental drivers of migration, by accounting for the interannual variation in covariate impact that was seen in this analysis.

Another notable limitation in our study was the absence of intrinsic factors. Factors such as age or body condition play an important role in migration behaviour and decision-making, and are themselves also intwined in the environmental factors that we examined (Newton 2012, Eggeman et al. 2016). Our study was limited by data availability, and while it is possible to propose inferences on their role in this system based on their interactions with extrinsic counterparts, confidence would be better placed in future research that is able to test movement models that incorporate both intrinsic and extrinsic factors.

Scale of analysis is also important to consider in movement ecology (McGreer et al. 2015, McNeill et al. 2020). It is important to appropriately fit the scale of an analysis to the scale of the desired behaviour, as well as ensure that all factors within the analysis match an overlying scale. This analysis included a collection of publicly available, satellite-based environmental data, with varying spatial and temporal scales, therefore it is possible that an imbalance of scales led to smoothing in the data, and may have obscured patterns present in the study sample.

5 Conclusion

These results challenge the generally accepted notion in Ontario that one caribou ecotype is strictly migratory and the other sedentary. Variation in both distance and probability of migration was observed across the study area, supporting the theory of flexible migration within woodland caribou. Several individuals demonstrated behavioural plasticity in response to environmental changes, particularly to snow cover. Additionally, while the cluster analysis supported the distinct grouping of forest-tundra and forest-dwelling ecotypes, those groupings did not coincide with spatial distribution of migration events. Behavioural plasticity makes migration an unreliable categorization criterion, and current categories that don’t take flexibility into consideration may be an oversimplification of their behaviour.

These are potentially positive results from a conservation standpoint, as environments change and ranges shift. It suggests that multiple behavioral strategies are successful within Ontario, and caribou may have previously unappreciated capacity to respond to future changes driven by climate warming or anthropogenic disturbance. That being said, both ecotypes are still in decline across Ontario (Vors et al. 2007, Newton et al. 2015), and require informed management in order to maintain sustainable populations. The results of this study provide additional information with which to inform management decisions, and aid in effective range management. Additionally, these results suggest that regardless of facultative or obligate migration strategy, caribou require unrestricted access to large amounts of open land in northern Ontario. While industrial development and habitat fragmentation have rarely been deemed a concern for the FT range, the potential for anthropogenically-imposed constraints on migration is an important consideration in future caribou conservation and management planning.

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APPENDIX

Table A1: Breakdown of GPS radio-collar data combined from three original sources. The combined dataset contained 88 caribou with two years of data and 21 caribou with three years. Final dataset was resampled to a consistent 25-hour fix rate.

Dataset	n	Collar type	Date range	GPS fix rate
1	65	GPS-ARGOS (Telonics Inc., 932 E. Impala Avenue, Mesa, AZ, 85204-6699, USA)	April 2009 – March 2011	5-hour and 25-hour intervals
2	35	GPS-ARGOS or GPS Iridium (Lotek Wireless Inc., Newmarket, ON, Canada)	April 2010 – March 2013	Variable
3	9	GPS Iridium (Telonics Inc., 932 E. Impala Avenue, Mesa, AZ, 85204-6699, USA)	April 2016 – March 2019	8-hour intervals

Table A2. Pairwise comparison of probability of migration analysis across pairs of years. GLMM was repeated using different years (1st and 2nd, 2nd and 3rd, 1st and 3rd) to evaluate how differences in years impacts model outcome. Models were reduced if necessary to converge. Statistical results of models found in Tables A3-5.

Model	Equation	n	AIC
All 3 years	Behaviour (1/0) ~ NDVI (summer) + Snow cover + Distance from Hudson Bay + Distance from roads + Latitude + Snow cover: Latitude + Individual (random)	241	155.6
Years 1 & 2	Behaviour (1/0) ~ NDVI (summer) + Snow cover + Distance from utilities + Distance from roads + Latitude + Longitude + Individual (random)	218	169.3
Years 2 & 3	Behaviour (1/0) ~ NDVI (summer) + Snow cover + Distance from roads + Latitude + Individual (random)	218	161.8
Years 1 & 3	Behaviour (1/0) ~ NDVI (summer) + Snow cover + Latitude + Individual (random)	218	167.7

Table A3. GLMM statistical output from probability of migration analysis using the first two years of each individual. Longitude (fixed) and Distance from Hudson Bay (fixed) terms were added, and Distance from Hudson Bay (fixed) and Latitude: Snow cover (interaction) terms were removed from the original model for model fitting. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	p-value	X^2
$\text{NDVI}_{\text{summer}}$ (Fixed)	**1.35 ± 0.68**	**1.98**	**0.048**	**-**
Snow cover (Fixed)	0.72 ± 0.62	1.18	0.23	-
Distance from utility corridors (Fixed)	16.63 ± 8.61	1.93	0.06	-
Distance from roads (Fixed)	1.56 ± 0.89	1.75	0.08	-
Latitude (Fixed)	1.66 ± 1.20	1.37	0.17	-
Longitude (Fixed)	1.18 ± 0.83	1.42	0.16	-
Individual (Random)	-	-	0.0004	24.88

Table A4. GLMM statistical output from probability of migration analysis using the Last two years of each individual. Distance from Hudson Bay (fixed), and Latitude: Snow cover (interaction) terms were removed from the original model for model fitting. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	p-value	X^2
$NDVI_{summer}$ (Fixed)	1.70 ± 0.93	1.83	0.066	-
Snow cover (Fixed)	**2.61 ± 0.79**	**3.31**	**0.001**	-
Distance from roads (Fixed)	1.25 ± 0.98	1.28	0.20	-
Latitude (Fixed)	1.37 ± 1.02	1.34	0.18	-
Individual (Random)			0.0001	23.21

Table A5. GLMM statistical output from probability of migration analysis using the first and third years of each individual. Distance from Hudson Bay (fixed), Distance from roads (fixed), and Latitude: Snow cover (interaction) terms were removed from the original model for model fitting. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	p-value	X^2
$NDVI_{summer}$ (Fixed)	**0.68 ± 0.41**	**1.66**	**0.097**	-
Snow cover (Fixed)	**1.15 ± 0.40**	**2.87**	**0.004**	-
Latitude (Fixed)	**1.10 ± 0.53**	**2.08**	**0.04**	-
Individual (Random)	-	-	0.00	22.41

Table A6. Pairwise comparison of migration distance analysis across pairs of years. LMM was repeated using different years (1st and 2nd, 2nd and 3rd, 1st and 3rd) to evaluate how differences in years impacts model outcome. All models were fitted with the same equation. Statistical results of models found in Tables A7-9.

Model	Equation	n	R^2C	AIC
All 3 years	Distance ~ $\text{NDVI}_{(\text{summer})}$ + Snow cover + Distance from Hudson bay + Distance from roads + Distance from utility corridors + Latitude + Longitude + Snow cover:Latitude + Individual (random)	205	0.75	4977.89
Years 1 & 2	Distance ~ $\text{NDVI}_{(\text{summer})}$ + Snow cover + Distance from Hudson bay + Distance from roads + Distance from utility corridors + Latitude + Longitude + Snow cover:Latitude + Individual (random)	187	0.71	4537.40
Years 2 & 3	Distance ~ $\text{NDVI}_{(\text{summer})}$ + Snow cover + Distance from Hudson bay + Distance from roads + Distance from utility corridors + Latitude + Longitude + Snow cover:Latitude + Individual (random)	183	0.74	4442.08
Years 1 & 3	Distance ~ $\text{NDVI}_{(\text{summer})}$ + Snow cover + Distance from Hudson bay + Distance from roads + Distance from utility corridors + Latitude + Longitude + Snow cover:Latitude + Individual (random)	183	0.73	4437.21

Table A7. LMM statistical output from distance of migration analysis using the first and second years of each individual. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	df	p-value	X2
NDVI$_{(summer)}$ (fixed)	-1.12 ± 8.66	-0.12	75	0.89	-
Snow cover (fixed)	**43.0 ± 5.97**	**7.19**	**75**	**0.00**	-
Distance from Hudson bay (fixed)	18.35 ± 14.51	1.26	75	0.21	
Distance from roads (fixed)	9.61 ± 7.53	1.26	75	0.21	-
Distance from utility corridors (fixed)	16.64 ± 8.61	1.93	75	0.06	-
Latitude (fixed)	**114.97 ± 17.29**	**6.65**	**75**	**0.00**	-
Longitude (fixed)	**64.67 ± 18.53**	**3.49**	**75**	**0.0008**	-
Snow cover:Latitude (interaction)	**59.83 ± 6.87**	**8.71**	**75**	**0.00**	-
Individual (random)	-	-	6	0.00	236.29

Table A8. LMM statistical output from distance of migration analysis using the second and third years of each individual. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	df	p-value	X2
$NDVI_{(summer)}$ (fixed)	-6.75 ± 8.98	-0.75	72	0.45	-
Snow cover (fixed)	**44.57 ± 5.91**	**7.54**	**72**	**0.00**	-
Distance from Hudson bay (fixed)	17.99 ± 15.65	1.15	72	0.25	-
Distance from roads (fixed)	10.66 ± 8.21	1.30	72	0.20	
Distance from utility corridors (fixed)	7.99 ± 9.28	0.86	72	0.39	-
Latitude (fixed)	**114.81 ± 17.83**	**6.43**	**72**	**0.00**	-
Longitude (fixed)	**63.86 ± 19.87**	**3.21**	**72**	**0.00**	-
Snow cover:Latitude (interaction)	**63.65 ± 6.89**	**9.23**	**72**	**0.00**	-
Individual (random)	-	-	**6**	**0.00**	**216.97**

Table A9. LMM statistical output from distance of migration analysis using the first and third years of each individual. Bold rows indicate statistical significance ($p < 0.05$). Significance of random effect determined using LRT test.

Variable (type)	β ± SE	Z-value	df	p-value	X2
NDVI$_{(summer)}$ (fixed)	-7.37 ± 8.57	-0.86	71	0.39	-
Snow cover (fixed)	**36.22 ± 5.83**	**6.21**	**71**	**0.00**	-
Distance from Hudson bay (fixed)	20.42 ± 15.05	1.36	71	0.18	-
Distance from roads (fixed)	7.92 ± 7.94	1.00	71	0.32	-
Distance from utility corridors (fixed)	8.61 ± 9.04	0.95	71	0.34	-
Latitude (fixed)	**117.26 ± 17.04**	**6.88**	**71**	**0.00**	-
Longitude (fixed)	**67.30 ± 19.08**	**3.53**	**71**	**0.0007**	-
Snow cover:Latitude (interaction)	**55.41 ± 6.68**	**8.30**	**71**	**0.00**	-
Individual (random)	-	-	**6**	**0.00**	**222.5**