

**RESEARCH ARTICLE**

Flexible migration by woodland caribou in Ontario, Canada

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Abstract

Recent studies of ungulate movement ecology suggest that seasonal movement tactics often vary within a population. The forest-tundra and forest-dwelling ecotypes of woodland caribou (*Rangifer tarandus caribou*) in Ontario, Canada, are traditionally presumed to differ in migratory strategy; however, their potential for facultative migration, the practice of interannual switching between migratory and non-migratory strategies, has yet to be explored. Understanding facultative migration, and any inherent variation and influences could help improve habitat management. We acquired global positioning system (GPS) telemetry-based movement data from 109 radio-collared caribou across the Hudson Bay lowlands between 2009 and 2019. We compared the data with estimates of vegetation density, snow cover, and human disturbance to identify environmental influences associated with the probability and magnitude of migration. We also compared seasonal resource selection between migratory and sedentary individuals. Caribou demonstrated plasticity in migration, with evidence of facultative migration by the forest-tundra and the forest-dwelling ecotypes. Variation in migration was likely a combination of local adaptation and acute response to changing environmental factors, particularly snow. Probability and distance of migration were positively correlated with snow, while distance also showed spatial dependency. Plasticity in migration has significant implications in relation to future shifts in climate and should be considered in relevant predictive analyses.

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KEYWORDS

behavioral plasticity, ecotype, environmental cue, movement ecology, *Rangifer tarandus*, resource selection, telemetry

Migration, broadly defined as cyclical movement between disjunct seasonal ranges (Fryxell and Sinclair 1988), can encapsulate a diverse range of behaviors, from highly variable, short displacements (Hofer and East 1993) to unwavering, population-wide, cross-continental flights (Alerstam et al. 2003). The shape and extent of migration is often influenced by the surrounding environment, with resource availability and competition often shaping the timing, duration, and distance of displacement (le Corre et al. 2017, Gurarie et al. 2019). Extrinsic and intrinsic factors can contribute to migratory variability, but the extent of influence by each factor on migration is highly variable across different species and not yet well understood.

Migration, particularly in ungulates, has historically been seen as an obligate behavior 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 predetermined by genetic constraints (Salewski and Bruderer 2007, Klütsch et al. 2016). Recent research, however, suggests that ungulate migration is not always a static, defining trait but rather a flexible, behavioral response to seasonally variable conditions (Eggeman et al. 2016, Xu et al. 2021). Facultative migration describes an optional behavior where individuals demonstrate behavioral plasticity, choosing to migrate or not based on external conditions such as weather and food availability, or internal factors such as age or body condition (Newton 2012). Evidence of more flexible forms of migration are seen across many taxa, including birds, fish, and mammals (Newton 2012, Shry et al. 2019, Xu et al. 2021).

A facultative or flexible migration strategy can improve access to energy in response to fluctuating environmental conditions (Nicholson et al. 1997, Milner-Gulland et al. 2011). Migration is a costly behavior because of the high energy expenditure of prolonged travel, and the increased risk of exposure to unknown threats or predation (Nicholson et al. 1997, Hebblewhite and Merrill 2009, Middleton et al. 2013). To be selectively advantageous, costs must be outweighed by the corresponding benefits, which are most often associated with seasonal resource availability and risk reduction (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2009, Fryxell and Holt 2013, Avgar et al. 2014, Kauffman et al. 2021). These trade-offs can determine whether a population migrates and how far they migrate (Teitelbaum et al. 2015). 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 allows for quicker response to less-predictable changes in resource availability (Jones et al. 2014, Teitelbaum et al. 2015). The same inconsistency and sudden environmental changes that may benefit facultative migrants would be costly to obligate migrants, who would make the journey regardless of conditions or cost (Devictor et al. 2008). In the face of increasingly volatile environments due to anthropogenic effects and climate change, flexibility in adaptive behaviors, such as migration, may be key to future survival. It is therefore important for conservation purposes to understand if and how individuals might be responding to changes in their environment, to maintain effective land use and protection plans.

The woodland caribou (*Rangifer tarandus caribou*) is a subspecies of caribou found across Canada (Committee on the Status of Endangered Wildlife in Canada 2011). They are a cold-adapted species that occupy a diverse range of ecosystems, with diet consisting of lichen, grasses, and woody shrubs in summer, switching predominantly to lichen in winter (Thompson et al. 2015, Webber et al. 2022). Two regional ecotypes are recognized in Ontario, Canada, based primarily on differences in migratory and calving behavior. Forest-tundra caribou are characterized by long seasonal migrations over thousands of kilometers to aggregate at calving grounds off the coast of Hudson Bay (Bergerud 1996, Abraham and Thompson 1998). Forest-dwelling caribou differ in behavior; the females remain in the boreal forest year-round, moving to isolated locations for calving rather than large communal calving grounds.

Forest-dwelling caribou are treated as sedentary, with much more limited seasonal movement compared to forest-tundra caribou (Cumming and Beange 1987, Bergerud et al. 1990, Berger 2004). Seasonal variation in range use is an important consideration for caribou conservation (Festa-Bianchet et al. 2011, Fraser et al. 2018, Weckworth et al. 2018). Certain features of caribou migration vary across Canada and Alaska, USA (Festa-Bianchet et al. 2011, Fullman et al. 2021), with different populations ranging from fully sedentary, to partially migratory (where only some individuals in each population migrate), to fully migratory (Committee on the Status of Endangered Wildlife in Canada 2011). Woodland caribou, particularly within the boreal forest, are generally considered sedentary in comparison to barren-ground caribou (*R. t. groenlandicus*), a northern subspecies known for extensive migrations (Theoret et al. 2022). More northern woodland caribou populations, however, have also been observed to be partially or fully migratory (Taylor et al. 2020).

While there is marked variation in migration across populations, facultative migration at the level of the individual has been little explored in woodland caribou. We investigated the potential for migratory plasticity in 2 ecotypes (forest-dwelling, forest-tundra) of woodland caribou. We hypothesized that migration is a flexible space use behavior in response to interannual variation in environmental constraints imposed by resource availability and winter intensity. By comparing migration events and caribou movement to corresponding environmental factors, we determined 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. Additionally, we compared seasonal resource selection between migratory and sedentary individuals to test the hypothesis that different land use strategies would confer differences in resource selection as well. If correct, individuals that migrate in a given year would demonstrate differences in resource selection compared to those that remained sedentary, and individuals that switch migration strategy between years will also demonstrate different patterns of resource selection between years.

STUDY AREA

In this study we examined movement data of woodland caribou from 2009-2019, ranging across a large portion of northern Ontario, Canada, with some overlap into the adjacent provinces of Manitoba and Quebec, spanning over 450,000 km². Subjects were located primarily within the Hudson Plains ecozone, extending into the Boreal Shield ecozone (Figure 1; Crins et al. 2009). Landscape varied considerably across the study area, ranging from heavily forested to barren tundra. The Hudson Plains ecozone is characterized by cold, short growing seasons, and extremely flat topography. Mean daily air temperatures ranged from -20°C to -27.5°C in January, and from 12°C to 16°C in July. Average annual precipitation ranged between 240 mm and 525 mm (Crins et al. 2009). Vegetation in the northern end was primarily coastal wetlands and open tundra dominated by sedges, lichen, dwarf birch (*Betula nana*) or willow (*Salix* spp.), with sparse forest consisting predominantly of black spruce (*Picea mariana*) and tamarack (*Larix laricina*; Ontario Ministry of Natural Resource and Forestry 2014). Coniferous forests, consisting of a mix of spruce (*Picea* spp.), tamarack, balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*), become more predominant farther south, merging into the dense, mixed forest of the Boreal Shield ecozone, additionally including hardwoods such as poplar (*Populus* spp.), beech (*Fagus* spp.), and eastern white cedar (*Thuja occidentalis*). There is greater variation in temperature and topography across the Boreal Shield, and annual precipitation varies from 500 mm/year in the west to 850 mm in the east. Elevation in the Boreal Shield is increased compared to the Hudson Plains, up to approximately 450 m. Predominant fauna include caribou, moose (*Alces alces*), and American black bears (*Ursus americanus*) in the Hudson Plains, with gray wolves (*Canis lupus*) and white-tailed deer (*Odocoileus virginianus*) as you move into the Boreal shield. Human activity was present through the study area primarily in the form of smaller communities (population <10,000), roadways, railways, and utility corridors, all of which become



FIGURE 1 Approximate study area (rectangle) and associated ecozones in Ontario, Canada. Telemetry data were collected from woodland caribou between 2009 and 2019, spanning a study area of approximately 450,000 km², encompassing a gradient of ecosystems. Caribou were located primarily in the Hudson Bay Lowlands ecozone, with some overflow into the Ontario Shield ecozone. Figure adapted from Crins et al. (2009).

less frequent farther north (Crins et al. 2009). Seasonal temperatures, precipitation, and predation pressure also decreased with increasing latitude. To account for the differences in summer growing seasons between ecozones, we operationally defined summer across the study area as 1 August to 30 September, fall as 1 November to 31 January, and winter as 1 February to 31 March. The spring calving season, from 1 April to July 31, was not investigated in this study.

METHODS

Classifying movement

To investigate variation in migration within caribou across Ontario, we analyzed previously collected movement data from 109 female woodland caribou fitted with global positioning system (GPS) telemetry collars from different parts of the province during 2009–2019 (Table S1, available in Supporting Information). Animal captures and

handling procedures were in accordance with Ontario animal care protocols (Avgar et al. 2015). To identify interannual variation in migratory behavior within an individual, we included individuals with a minimum of 2 consecutive years of movement data. The final dataset consisted of 89 individuals with 2 years of GPS data, and 20 individuals with 3 years of data. We eliminated notable outliers in movement (i.e., isolated spikes in distance between individual fixes, or round trips at unreasonable speeds), and then resampled data to fixes at 25-hour intervals to standardize sampling rate.

In this study, we chose to focus our investigation on fall migration, to contribute to a more complete understanding of seasonal cycles of movement. Many studies of migration in caribou in Ontario specifically focus on spring migration, from the winter range to the spring calving grounds, in part because of the importance of calving behavior in categorization of the local ecotypes (Bergerud et al. 1990, Pond et al. 2016). Predator avoidance and forage availability are primary forces behind spring migrations (Viejou et al. 2018), but it is less established what influences caribou to leave low threat areas to return to their wintering range.

We used seasonal range separation to define migration and categorized caribou into ecologically significant movement classes. To calculate seasonal ranges, areas used between migration events, we partitioned spatial fixes into summer and winter seasons. To reduce the chance of a false negative prediction of migration, we chose the least active months to calculate seasonal ranges based on the monthly averages of net squared displacement (NSD; Figure 2). Higher mean NSD indicates greater movement and therefore greater chance of a migration event. Conversely, lower mean monthly NSD indicates low activity months, in which migration is less likely to occur. For each seasonal range, we used kernel density estimation on the movement data during each defined season to calculate seasonal (95%) utilization distributions (Fieberg and Kochanny 2005). We performed all calculations in R version 4.0.3 (R Core Team 2019) using the package amt (v0.2.1.0).

To identify instances of migration, we calculated seasonal range overlap between consecutive summer and winter utilization distributions using a utilization distribution overlap index. We identified a migration event by the complete absence of overlap between summer and winter ranges (utilization distribution overlap index = 0). Based on patterns of range overlap over multiple years, we then grouped individuals into 4 classes: obligate migratory, facultative migratory, sedentary, or nomadic. Obligate migratory individuals exhibited consistent, annual migrations, with site fidelity to at least the summer range (Hazell and Taylor 2011, Berglund et al. 2014). We classified individuals with consistently overlapping seasonal ranges (no migration) as sedentary, and individuals that exhibited a mix of migratory and sedentary strategies (i.e., overlapping ranges in some years but not others) as facultative migratory. We classified individuals as nomadic if they exhibited separation between seasonal ranges but did not

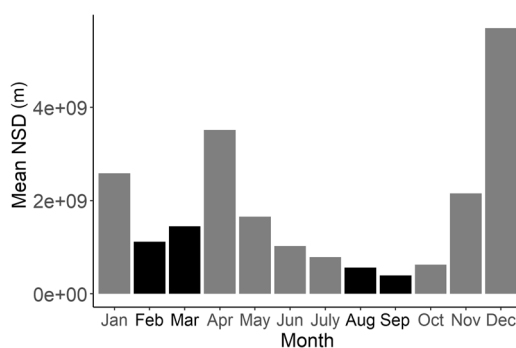


FIGURE 2 Mean monthly net squared displacement (NSD) for woodland caribou in Ontario between 2009 and 2019. We averaged daily NSD (m) each month and across all individuals to identify high and low activity periods throughout the year. We then used telemetry data from the low activity months, August and September for summer ranges and February and March for winter ranges (darker bars), to calculate resident seasonal range estimates.

exhibit site fidelity to winter or summer ranges. We used the terms obligate migratory or sedentary to operationally define individuals based on the behavior exhibited within the 2- to 3-year dataset. A longer dataset is required to confidently determine whether individuals are truly obligate migratory or sedentary.

Environmental correlates of migration

To better understand the potential benefits of movement, we evaluated the effects of environment on annual movement patterns. We examined several environmental covariates, chosen based on their demonstrated impact 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). We averaged covariates for each individual each year across either a summer, winter, fall, or annual home range, calculated using Brownian bridge estimation based on seasonal or annual movement (Horne et al. 2007). We then used these covariates to investigate how the environment influences the probability of migration occurring and the distance of migration when it did occur.

As an index of forage availability and vegetation density, we used normalized difference vegetation index (NDVI). The NDVI is based on remotely sensed estimates of visible and near-infrared wavelengths whose ratio is correlated with vegetation green biomass (Pettoirelli et al. 2005). Areas of high NDVI may provide increased food energy for migration but also potentially provide less incentive to migrate in the first place (Avgar et al. 2013). High levels of vegetation abundance could also be associated with reduced habitat permeability, which would increase the energetic cost of migration and make prolonged migratory movements less favorable.

We acquired NDVI remote sensing data (16-day temporal resolution, 500-m spatial resolution) from the Land Processes Distributed Active Archive Center (Didan 2015). 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 performed additional cleaning on the raster data by removing pixels with low pixel reliability scores. We determined mean summer NDVI for each individual each year by averaging NDVI layers temporally across the 9 layers that fell within the summer period, and then averaging pixel values spatially across the determined summer range.

Weather and climate are often strong influences of migration also (le Corre et al. 2017, Cameron et al. 2021, Pedersen et al. 2021). Heavy snow, for example, increases the energetic cost of movement, making long migrations more costly (Mosser et al. 2014). Snow cover can also be associated with reduced forage availability (Avgar et al. 2013). This lack of available resources may force individuals to relocate regardless of cost of movement.

For snow cover, we used snow water equivalent (SWE) as a proxy, defined as the depth (m) of melted water equivalent to snowpack (Vionnet et al. 2021). The SWE takes density of snowpack into consideration, so it is useful as a measure of winter intensity and foraging difficulty for caribou, as caribou must dig craters to access food in deep snow (Pedersen et al. 2021). With snow depth also considered, this measurement is also linked to the energetic cost of travel (Avgar et al. 2013). Through either obstruction to foraging or increased cost of movement, increased SWE correlates with an energetic loss to caribou (Mosser et al. 2014). We acquired SWE raster layers from the ERA5-land dataset at 0.1-degree (~11 km) spatial resolution, and then averaged daily estimates from the fall and winter season each year across the annual and winter home ranges, respectively, to obtain seasonal (fall, winter) estimates of snow cover (Muñoz-Sabater 2019).

In addition to measures of vegetation and snow, we included several measures of human disturbance, such as distance from roads, railways, and utility corridors, to test the impact of human activity on migration. Caribou treat human activity similar to other perceived threats and often 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, van Moorter et al. 2020). Proximity to human disturbance may influence whether an animal migrates or not.

We obtained spatial layers for roadways, railways, and utility corridors from the Ontario Geospatial Data Exchange (2021). To measure broad-scale patterns of movement in relation to these features, we converted the spatial layers from presence-absence to a proximity-based metric. We converted vector layers to raster layers at a 500-m resolution in ArcGIS (Esri, Redlands, CA, USA), with each grid pixel containing values representing proximity to the linear feature. This allowed us to test at a broad scale how distance from human activity correlates with migratory behavior. We averaged proximity values across the entire annual home range of each individual to obtain an estimate of proximity to human infrastructure.

We processed all spatial layers in ArcGIS Desktop version 10.8.1 (Esri) and R version 4.0.3 (R Core Team 2019). We converted all layers to z-scores to standardize the different scales and units of measure.

We formulated several linear mixed models to investigate the effect of the environment on the probability and distance of fall migration. Specifically, we tested whether location of seasonal range (represented by latitude, longitude, and proximity to the coastline of Hudson Bay) or vegetation (measured by NDVI), winter intensity (as indexed by SWE), and human disturbance (infrastructure and linear features) within a seasonal 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 the distance of migration, as measured by the distance between winter and summer home range centroids. We performed all statistical analyses in R.

To estimate the effect of environmental conditions on the likelihood of fall migration within a given year, we performed a generalized linear mixed model (binomial family, logit link). We included all individuals in this analysis, each with 2–3 migration events per individual ($n = 238$). We included seasonal range estimates of vegetation, snow cover, and human disturbance in the model, along with spatial measures of latitude, longitude, and distance of seasonal ranges from the Hudson Bay coastline. We included individual as a random effect to account for repeated sampling across individual caribou and for imbalance in sampling among individuals (Gillies et al. 2006). We tested collinearity by comparing pairwise correlations for all variables. Based on the methodology of Dormann et al. (2013), we excluded 1 variable of each collinear pair exceeding a threshold of $|r| \geq 0.6$ from the analysis. We made the decision of which variable per collinear pair to exclude based on Akaike's Information Criterion (AIC) comparison. We then tested model parsimony using AIC, opting for the model with lowest AIC. We also tested the model for overdispersion and linearity; the final model met all assumptions.

To estimate how environmental factors affect variability in migration distance, we ran a linear mixed effects model. We combined individuals that were identified as obligate migratory with the migratory years of nomadic or facultative migratory individuals for this analysis, to include all recorded instances of migration ($n = 158$). We estimated migration distance as the linear distance between centroids of summer and winter ranges. We calculated centroids for both ranges in R using the package *amt* (version 0.2.1.0). We compared distance in the model against the same environmental metrics as the previous analysis, with the most parsimonious model chosen based on AIC. We maintained individual as a random effect to account for repeated sampling. The final model met all assumptions of linearity, independence, absence of outliers, and normality of residuals. The model did not pass the assumption of homogeneity of variance of the residuals (Breusch-Pagan test, $BP_{(8)} = 37.7$, $P < 0.001$). We still used a linear mixed effects model, as they have shown robustness to violations of this assumption, and while heteroscedasticity affects the precision of estimated errors, it should not bias the model (Schielzeth et al 2020).

Comparing seasonal resource selection and migration behavior

Following our analysis on the environmental determinants of probability and distance of migration, we calculated seasonal resource selection functions (RSF) for each caribou to examine whether patterns of selection between individuals, or between years within a single individual, mirrored differing patterns of migratory behavior. We modeled seasonal RSFs on the first 2 years of data for individuals from 2009 to 2013, excluding individuals from 2014–2019 because of low sample size per year.

We included previously used landscape layers such as vegetation and snow cover in the model, and added land cover type to test for differences in more general habitat selection. We used land cover classes taken from the Far North Land Cover (version 1.4, spatial resolution = 30 m) dataset provided by the Ontario Ministry of Natural Resources and Forestry (2014). Following the methodology of Avgar et al. (2013), we aggregated the original 24 classes in the dataset to form 7 broader classes based on dominant vegetation, each with distinct benefits and energetic consequences for caribou (Table S2, available in Supporting Information).

We calculated separate resource selection functions for summer and winter seasons and for fall migration. We examined selection at the level of the seasonal home range by calculating a minimum convex polygon based on the used GPS points within the seasonally subdivided movement data, and then generating 1,000 random available points within this broad seasonal range, for each individual, each year. We fit a logistic regression to compare covariates between used and available points and determined measures of selection for environmental covariates.

To compare selection and migration tendencies, we extracted selection coefficients with $P < 0.05$ (representing attraction to or repulsion from various landscape features) for all covariates for each individual. We then compared patterns of selection between individuals of different migratory classes and across years using a 2-way repeated measures analysis of variance. We also performed a 1-way repeated measures analysis of variance to compare selection between years of facultative individuals. We calculated type II sums of squares to account for unbalanced sample sizes between groups. We performed *post hoc* pairwise t-tests on the strongest results ($P < 0.05$). We analyzed all data in R, using packages *amt* (version 0.2.1.0) and *lme4* (version 1.1-35.2).

RESULTS

Of the 109 caribou sampled in the James Bay basin, 35.8% were categorized as obligate migratory, 47.7% as facultative migratory, 10.1% as sedentary, and 6.4% as nomadic (Figure 3). All migration strategies occurred throughout the study area.

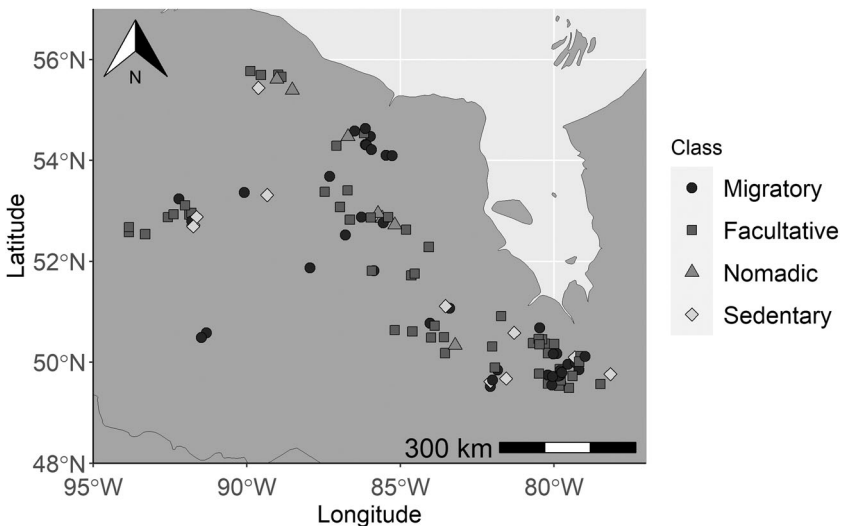


FIGURE 3 Spatial distribution of woodland caribou movement classes across northern Ontario, Canada. Points represent the centroid of the winter range from the first year of observation of each individual, 2009–2019. We observed all migratory classes distributed across the study area.

We found annual variability in migration strategy within individual migrants across the entire study site. Individuals in the north showed the greatest variation in annual movement (Figure 4); one of the longest migration distances recorded from a facultative individual was 404.6 km in a migratory year, nearly 6 times greater than the previous sedentary year where the distance between seasonal ranges was 68.3 km. Within the forest-dwelling caribou region, there was less difference in travel distance for facultative individuals between migratory and sedentary years than in the northern (forest-tundra) region. Migration distance for individuals below 52° latitude never exceeded 200 km, with an average migration distance of 55.3 km.

The majority of facultative migratory individuals tended to demonstrate the same movement behavior in a given year (Table 1). In 2009, 94% of observed facultative individuals demonstrated sedentary behavior, while in 2010, 92% migrated. This pattern continued in subsequent years, with $\geq 80\%$ of the facultative population each year exhibiting the same behavior.

Following AIC comparison of candidate migration probability models (Table S3, available in Supporting Information), all top-ranking models included snow as a predictor of migration; probability of migration was positively associated with increase in SWE during fall ($\beta = 0.86 \pm 0.22$ [SE], $P < 0.001$; Figure 5). Effect sizes indicated snow was the strongest predictor of migration and migration showed no correlation with location (latitude, longitude, proximity to Hudson Bay coastline), NDVI, or proximity to human disturbance ($P > 0.05$; Table S4, available in Supporting Information).

For the migration distance model, the top-ranking model based on AIC comparison included covariates relating to vegetation, location, snow cover, and human disturbance (Table S5, available in Supporting Information). Like the

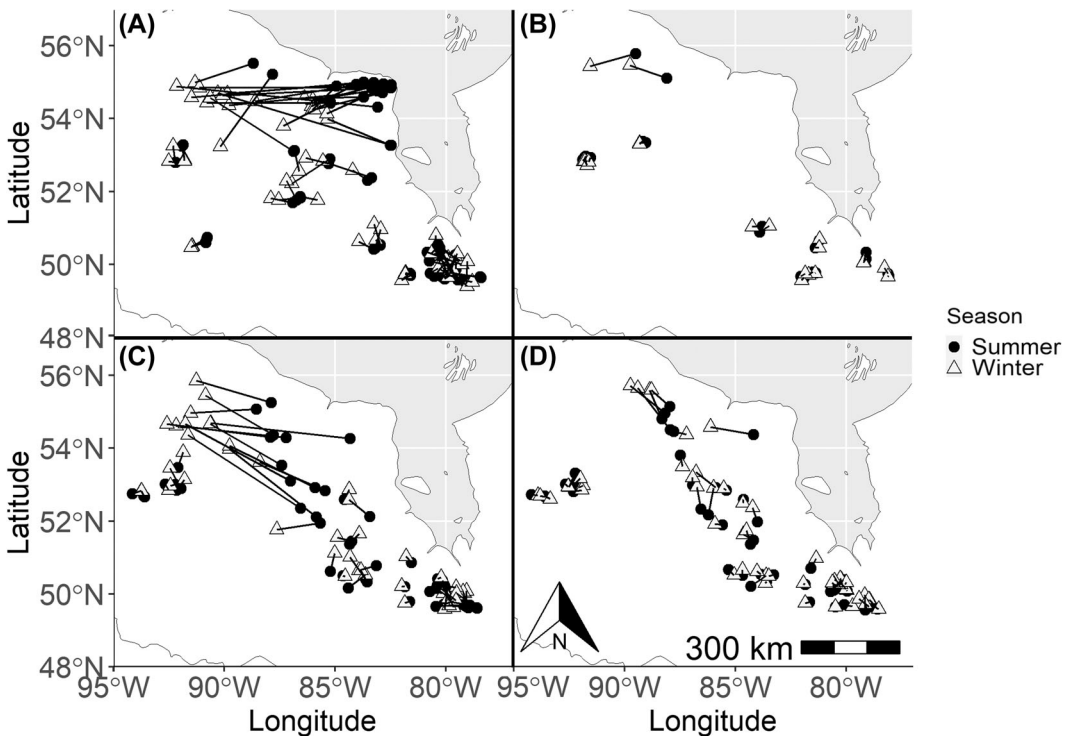


FIGURE 4 Range separation of woodland caribou across northern Ontario, Canada between 2009 and 2019. Individual caribou were categorized as obligate migratory ($n = 39$; A), sedentary ($n = 11$; B), and facultative migratory ($n = 52$; split into migration years [C] and sedentary years [D]) classes. Lines represent the linear distance between the centroids of a given summer range and the consecutive winter range. For migratory individuals, this distance correlates with migration distance.

TABLE 1 Contingency table depicting frequency distribution of migratory or sedentary strategies of facultative migratory woodland caribou for each year of study in 2009–2019 in Ontario, Canada. Facultative migratory caribou used both migratory and sedentary strategies between the 2–3 years of observation.

Year	Migration strategy	
	Migratory	Sedentary
2009	2	29
2010	36	3
2011	2	14
2012	14	2
2016	0	5
2017	4	1
2018	5	0

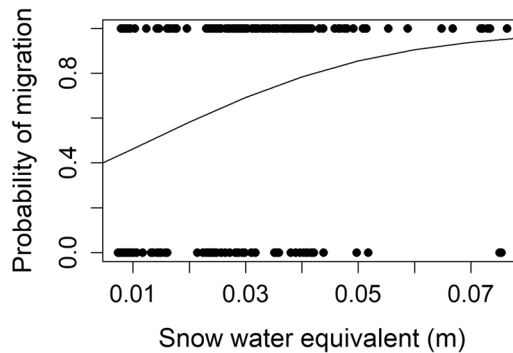


FIGURE 5 Estimated probability of annual migration of woodland caribou in Ontario, Canada, in relation to mean snow water equivalent (m). Snow water equivalent was averaged across the home range of each individual from 1 November to 31 January of each year between 2009 and 2019.

probability model, this model showed strong evidence that distance was correlated with fall SWE ($\beta = 21.47 \pm 5.74$, $P < 0.001$; Figure 6), and showed no correlation with NDVI or proximity to roads or utility corridors ($P > 0.1$; Table S6, available in Supporting Information). Additionally, there were spatial trends in migration distance, as migration distance was correlated negatively with latitude ($\beta = -68.28 \pm 18.82$, $P < 0.001$), longitude ($\beta = -183.40 \pm 21.20$, $P < 0.001$), and distance from Hudson Bay ($\beta = -123.61 \pm 13.23$, $P < 0.001$). Conditional R^2 for the model, calculated using MuMIn package (version 1.46.0) based on the methods in Nakagawa et al. (2017), was 0.83.

We determined estimates of selection for NDVI, snow cover, and land cover for each individual with a resource selection model. Comparing selection coefficients across individuals, selection for NDVI and snow varied, with evidence of positive, negative, or no selection (mean selection coefficients: NDVI = 0.0005 ± 0.001 , snow_(fall) = -76.45 ± 962.45 , snow_(winter) = 145.91 ± 966.83 ; Figure S1, available in Supporting Information). In examining seasonal selection for land cover, individuals demonstrated positive selection for all land cover classes, apart from water, across all seasons, although there was some variation in strength of selection between land cover classes (analysis of variance, fall: $F_{5, 258} = 6.69$, $P \leq 0.001$; winter: $F_{5, 114} = 8.09$, $P \leq 0.001$; Figure 7). In particular, selection

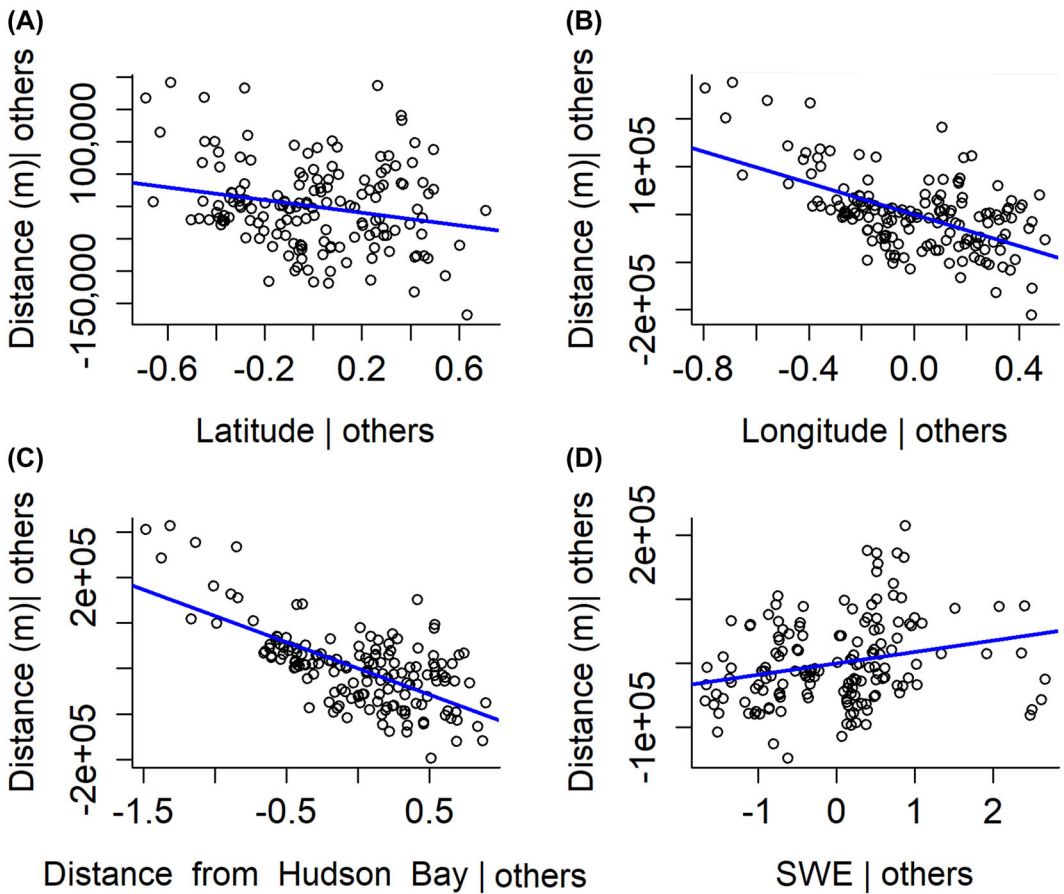


FIGURE 6 Partial regression plots displaying distance traveled (m) by woodland caribou in Ontario, Canada, in relation to latitude (A), longitude (B), distance from Hudson Bay (C), and mean snow water equivalent (SWE; D) of the winter home range. Each plot represents the partial effect of a given explanatory variable when all other variables are held constant. All explanatory variables were standardized to z-scores before analysis, therefore variables on the x-axis are all on the same unit of measure.

for lowlands was at least 39% lower than other land cover classes in both fall and winter seasons (Table S7, available in Supporting Information).

Across migratory classes, patterns of selection for land cover were statistically similar, with the exception of selection for lowlands during the fall season ($F_{3,73} = 7.77$, $P \leq 0.001$). During this season, while all classes demonstrated positive selection for lowlands, sedentary individuals showed a >50% increase in selection strength compared to any other class (pairwise t -test: $P_{(\text{sedentary-obligate})} = 0.001$, $P_{(\text{sedentary-facultative})} = 0.004$, $P_{(\text{sedentary-nomadic})} \leq 0.001$). There were no other differences in selection for any other land cover classes, or between years. There was no evidence of differences in selection for NDVI or snow between migration classes or between years within any class.

DISCUSSION

Caribou in this study demonstrated greater flexibility in annual migration behavior than has been previously recorded in Ontario. While some variability in distance of migration was correlated with location, and likely ecotype, environmental factors also played a role; in particular, probability and distance of migration were correlated with

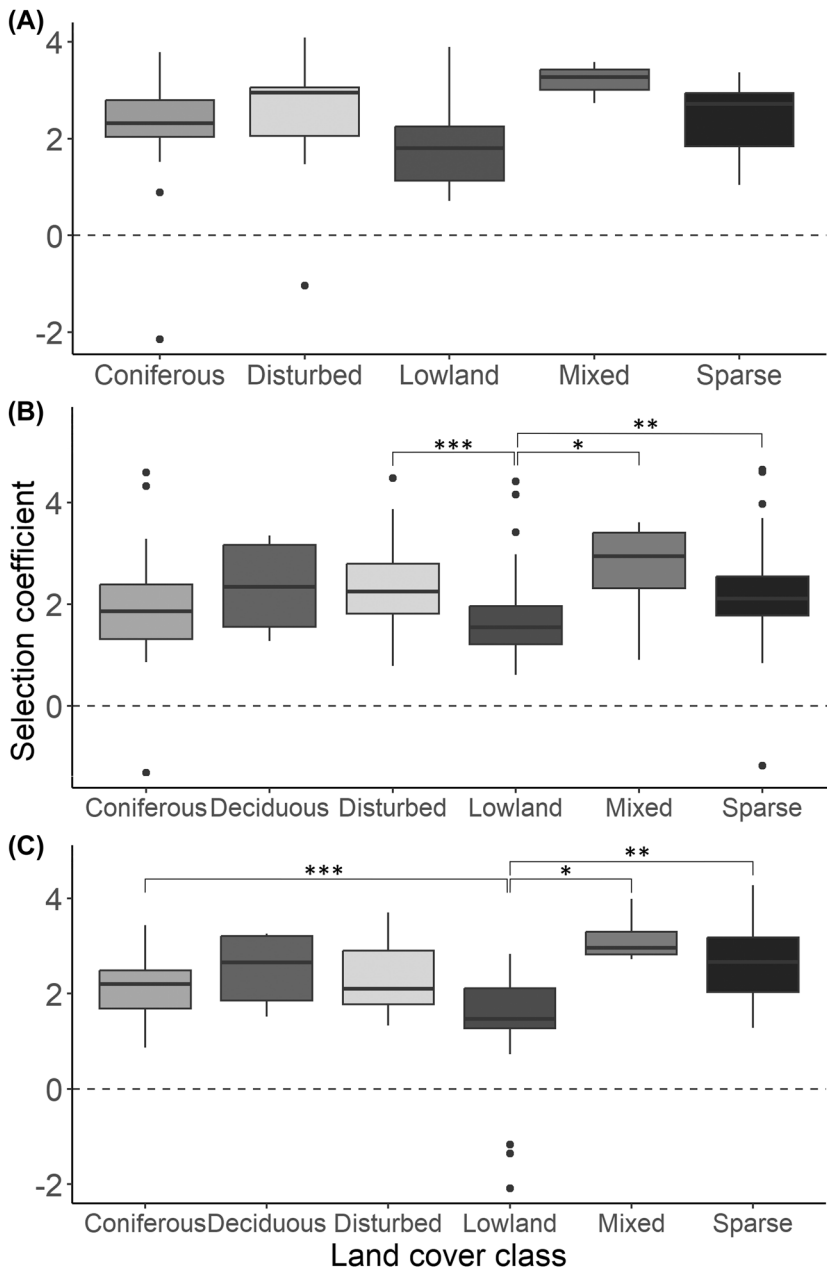


FIGURE 7 Boxplots of selection coefficients for land cover class for summer (A), fall (B), and winter (C) seasons for each year. We calculated resource selection functions for 109 woodland caribou in Ontario, Canada between 2009 and 2013. Asterisks denote strong evidence of differences between covariate pairs ($P < 0.05$).

snowfall during migration. While these patterns did not translate further into range-level patterns of resource selection, these results support the hypothesis that migration in ungulates can be a flexible response to acute environmental stimuli.

Others have reported 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 (*Cervus canadensis*; Eggeman et al. 2016), mule deer (*Odocoileus hemionus*; 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 (*Bison 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 weather variation, while additionally revealing a population-wide pattern of decision-making that has not been thoroughly documented.

Our research suggests the potential for population-wide patterns in broad-scale movement among facultative migratory individuals. Many facultative individuals undertook the same behavioral strategies across several years: the majority did not migrate in 2009 or 2011 and did migrate 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 influenced 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 most facultative individuals undertook migration coincided with greater mean annual SWE (Figure 8). Strong conclusions cannot be drawn because of the low sample size (2-3 years per individual), but the pattern suggests that these individuals chose to migrate each year in response to external stimuli, such as snowfall. This pattern is particularly interesting within forest-dwelling 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 influenced consensus but rather a shared trait across individual caribou in response to a common environmental stimulus.

Variability in both frequency and intensity of migration in caribou occurred across our entire study range, even at the north end within the established range of the forest-tundra ecotype (Figure 3). These northern individuals demonstrated divergence from the classic forest-tundra caribou definition of long migrations up to thousands of kilometers to the Hudson Bay coast (Bergerud 1996). While some individuals migrated over 500 km to calve right on the coast, others traveled less than half that distance and settled farther inland on the Hudson plains. Even at the southern end of the study range where migration distance was more muted, with an average of 55 km between seasonal ranges, some migrations spanned over 100 km.

Distinct behavioral differences between the ecotypes broke down further in overlap areas between the 2 ecotype ranges. Within the area of range overlap, caribou demonstrate intermediate migration distances, and equal

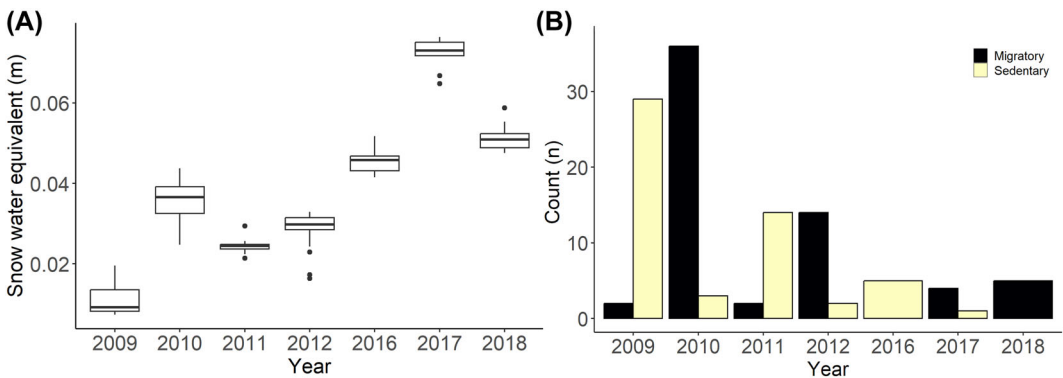


FIGURE 8 Annual variation in (A) mean snow water equivalent (m) across winter ranges of woodland caribou, and (B) occurrences of each migration strategy in facultative migratory woodland caribou in Ontario, Canada, 2009–2018.

potential for facultative migration. Similar intermediate behavior was observed in a previous study on a small subset of caribou located near the boundary between ecotypes (Hazell and Taylor 2011). 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.

Resource selection functions were also ineffective in delineating caribou into behavioral groups. While there was considerable variation in patterns of resource selection for vegetation, snow, or land cover, it is as of yet unclear what prompts this variation in selection. It is possible that resource selection associated with migration operates on a different scale of analysis, such as a finer scale step selection. Regardless, these results demonstrate that range-level patterns of resource selection do not translate into seasonal migration behaviors. Overall, our results indicate that this behavior is likely a combination of both local adaptation and acute environmental response.

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). Previous studies on caribou in the Arctic have also reported that snow influences annual patterns of habitat selection and movement (Cameron et al. 2021, Pedersen et al. 2021). Similar trends of increased migration with greater snow cover or winter intensity have also been previously seen in roe deer (*Capreolus capreolus*) and mule deer, both species of which food sources are similarly limited by snow (Nicholson et al. 1997, Cagnacci et al. 2011). Our findings support the previous literature in demonstrating that migration in ungulates is not a static behavior and is altered annually in response to acute conditions such as weather or snow.

Vegetation and human disturbance demonstrated little effect on migration, in contradiction to our hypothesis. We did not observe an effect of NDVI or proximity to linear features on probability or distance of migration, despite both having been shown in past studies to influence caribou space use behavior in several ways (Avgar et al. 2013, Beyer et al. 2016, Prokopenko et al. 2017). There could be several factors that caused this result because of the complexity of the relationship. Patterns of selection and habitat use may differ based on the scale of analysis; therefore, it is possible this analysis may be too broad-scale to pick up these relationships. Alternatively, NDVI may not be an accurate representation of caribou winter diet, because NDVI cannot directly identify lichen, and it would not register ground lichen buried under snow. There is a lack of precise vegetation and remote sensing coverage in the far north region of Ontario, which limits the complexity of models for northern caribou. As a result, there is a lot we still do not know about the behavior of those individuals in relation to their environment.

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 behavior in terms of time, energy, and survivorship, and is accordingly 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 blocks off key migratory routes, or as changes in climate lead to phenological asynchrony (Berger 2004, Mayor et al. 2017). As a result, behavioral plasticity is increasingly viewed as an important ingredient for persistence (Mayor et al. 2017, Severson et al. 2021, Xu et al. 2021).

MANAGEMENT IMPLICATIONS

These results challenge the generally accepted notion that caribou in Ontario are strictly migratory or sedentary. Behavioral plasticity in caribou may confer resilience to changing environments, or it may indicate the potential for future behavioral shifts. Changes in migration in response to snow suggest that the behavior may shift as the climate shifts; moderate winters may even lead to loss of this strategy. This relationship between movement and climate should be considered in future movement models and research.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal captures and handling procedures were in accordance with Ontario animal care protocols. Animal utilization protocols during 2009–2013 were approved by Ontario Ministry of Natural Resources (permits 10/11/12-218 and 10/11/12/13-183). Animal care protocols for 2016 were approved by the Wildlife Animal Care Committee (permit 16-354).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.24546370>.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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