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ARTICLE

Animal Ecology

The influence of environmental conditions on the selection of spring migration routes by caribou

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Abstract

Animal migrations influence key ecological processes such as predator–prey dynamics, nutrient and energy cycling, and community structure. Long-distance migrations are declining worldwide, and a better understanding of the factors influencing animal space use during migrations is essential to maintain this behavior in the wild. We mapped the spring migration routes used by female caribou of the declining Rivière-aux-Feuilles herd in northern Québec, Canada, from 1994 to 2019. We used resource selection functions to determine the effect of remotely sensed measures of snow depth, precipitation, elevation, and land cover classes on habitat selection along 811 migration routes used by 304 individuals. We further explored whether observed trends in the geographic position of migration routes (e.g., mean longitude, mean variance of longitude) influenced calf recruitment the following fall. Female caribou selected areas with deeper snow, less precipitation, and lower elevation, avoided forest and lichen heath, and selected more strongly erect-shrub tundra and waterbodies than the reference category, shrub tundra. A cluster analysis revealed different migration patterns, with migration routes in the early 2000s being more restricted in space and located further inland than routes in the 2010s. The location of spring migration routes was unrelated to changes in calf recruitment. The characterization of migration routes used by caribou will help inform management and could be used to predict future herd movements in response to different climate change scenarios.

KEYWORDS
animal migration, habitat selection, migration corridor, migratory caribou, northern Québec, *Rangifer tarandus*, resource selection function

INTRODUCTION

Animals in seasonal environments must cope with variations in resource quality and availability. Some species have the capacity to move over large geographic distances, increasing the window of opportunity during which high-quality resources are available to them (Kauffman et al., 2021). These migrations, albeit energetically costly (Fancy & White, 1987), improve the survival and reproduction of migrants by increasing their foraging opportunities as well as reducing predation risk (Fryxell & Sinclair, 1988; McKinnon et al., 2010). Migrations are performed by many taxa, from zooplankton (Haney, 1988) to blue whales (*Balaenoptera musculus*; Mate et al., 1999), and from monarch butterflies (*Danaus plexippus*; Nebel, 2010) to pronghorns (*Antilocapra americana*; Sawyer et al., 2005). The length of migrations can vary, from relatively short distances (e.g., the summer and winter ranges of Eurasian blue tits *Cyanistes caeruleus* in Sweden can be less than 50 km apart, Nilsson et al., 2008) to almost three times the diameter of the Earth (e.g., Arctic terns *Sterna paradisaea* travel on average 34,600 km during their southbound migrations; Egevang et al., 2010).

Long-distance migrations involve complex individual behaviors that can vary through time. For instance, Eggeman et al. (2016) showed that the decision to initiate migration in elk (*Cervus elaphus*) was density-dependent, with a greater number of individuals migrating during periods of high conspecific density. These authors also found that the individual propensity to migrate varied from year to year, mirroring changes in environmental conditions. Such behavioral plasticity could be beneficial to individuals, for example, by allowing them to track vegetation phenology (Horton et al., 2020; Laforge et al., 2021, 2025; Le Corre et al., 2020), thereby increasing fitness (Taylor & Norris, 2007). Behavioral plasticity also translates into individuals modifying their migration routes or destination in response to adverse weather conditions or physical barriers (Sawyer et al., 2009; Xu et al., 2021). Populations comprising individuals that are able to adjust their migratory behavior should be more resilient to environmental changes (Gilroy et al., 2016), although counterexamples exist in the wild (Xu et al., 2021).

Long-distance migrations are declining worldwide (Tucker et al., 2018), either through migratory population declines or from individuals being unable to migrate due to human development or climate change (Bolger et al., 2008; Robinson et al., 2009). This trend is particularly severe in urban and peri-urban environments (Cusa et al., 2015; Tucker et al., 2018), but migrations of wild-ranging species, such as several species of ungulates, are also under threat (Kauffman et al., 2021; Lamb et al., 2025). In the Arctic, climate change could hinder the migrations of migratory caribou (*Rangifer tarandus*) by modifying the quality and availability of snow and ice as substrates for movement (Leblond et al., 2016). Different climate regimes could also modify the abundance of biting flies (Witter, 2010), the availability of forage (Zamin et al., 2017), or the frequency of extreme weather conditions during long-distance migrations (Putkonen & Roe, 2003). Together, these could potentially alter caribou behavior and ultimately population demography (Mallory & Boyce, 2018). Determining environmental factors influencing selection of migration routes and resulting consequences on vital rates at the population level is key to improving the management and conservation of migratory species living in a changing climate (Horne et al., 2007).

Migratory caribou is one of the most vagile terrestrial species in the world (Joly et al., 2019; Wilcove & Wikelski, 2008). They can have a strong influence on plant communities in the Arctic, occurring in herds of hundreds of thousands of individuals that both forage and trample the vegetation in low-productivity tundra (Festa-Bianchet et al., 2011; Morrissette-Boileau et al., 2018). In northern Québec, Canada, the Rivière-aux-Feuilles caribou herd performs seasonal migrations over 1000 km (Le Corre et al., 2020; Leblond et al., 2016). Around April, individuals leave wintering grounds in the boreal forest to get to their northern calving grounds, which they reach in early June (Le Corre et al., 2020; Leclerc et al., 2021). Most adult females migrate while pregnant, after depleting most of their body reserves during the winter (Adamczewski et al., 1993). The spring migration is thus a decisive period that may determine the reproductive success of individual female caribou. Studies conducted in this system showed that migrating caribou avoided ice-free lakes (Leblond et al., 2016), selected tundra at low elevation (Leclerc et al., 2021), and arrived later on calving grounds when temperatures were mild and precipitation was abundant (Le Corre et al., 2017). The environmental characteristics determining the location of caribou migration routes at a broad spatial scale, however, are not well understood.

In this study, we mapped the migration routes used by adult females of the Rivière-aux-Feuilles caribou herd during the springs of 1994–2019, leveraging a longitudinal dataset of 304 GPS-collared caribou. We focused on spring migrations because of their strong link to female reproductive success, as described above. Moreover, the movements of individuals during fall migrations are much more convoluted, partly due to long pauses occurring during the rut (Le Corre et al., 2017). Along spring migration routes, we performed habitat selection analyses to explore the influence of weather, snow conditions, topography, and land cover type on caribou space use. We hypothesized that external factors influence the location of migration routes selected by caribou. More specifically, we predicted that lichen-rich areas (lichen heath) would be selected by caribou, because lichens are the primary food source for caribou at that time of year (Webber et al., 2022). We also predicted that caribou would select areas with shallower snow depth (Fancy & White, 1987), less precipitation (Le Corre et al., 2017), and lower elevation (White & Yousef, 1978) to minimize energy expenditures during locomotion. Finally, we explored whether the geographic position of spring migration routes varied annually and tested whether these variations were linked to changes in calf recruitment the following fall (i.e., ~6 months later). As spring migration occurs just before the calving period, we hypothesized that the migration routes used by pregnant females would influence their energy expenditures, which would translate to variable calf recruitment.

MATERIALS AND METHODS

Study area

During the study period (1994–2019), the distribution of the Rivière-aux-Feuilles caribou herd covered approximately 450,000 km^2 in northern Québec, Canada. The size of the population varied during that time, from an estimated 276,000 individuals in 1991, to more than 650,000 in 2011, and then back to an estimated 199,000 in 2016 (Taillon et al., 2016). Survival and recruitment estimate after 2016 suggested that the abundance was relatively stable or slowly decreasing in more recent years (Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs [MELCCFP], unpublished data). The wintering grounds of the Rivière-aux-Feuilles caribou herd were mostly composed of black spruce (*Picea mariana*) with an understory of shrubs and lichens (Latifovic & Pouliot, 2005). The calving and summer grounds were dominated by *Salix* and *Betula* shrubs, graminoids, and lichens. The topography of northern Québec is relatively flat, with a maximum elevation of approximately 1000 m. The climate is typical of arctic and subarctic zones, with long, cold winters followed by short, cool summers (Berteaux et al., 2018). The mean annual temperature was −3.6°C and the mean annual precipitation was 1077 mm, falling mostly as snow between the months of October and April.

Caribou capture and monitoring

Between 1994 and 2019, experienced technicians from the Québec government captured 304 female caribou using a net gun fired from a helicopter (Bookhout, 1996) and fitted them with GPS collars. Captures and handling of animals followed guidelines from the Animal Care Committees of MELCCFP (CPA-18-04; 19-03) and Université Laval (permit numbers 20090513, 2011039, 2018033-1). From 1994 to 2010, most collars were ARGOS Telonics (Mesa, USA) programmed to collect a location every 5 days. Then, between 2011 and 2019, Vectronics Aerospace collars (Berlin, Germany) using Iridium or Globalstar networks collected a location every 13 h or more frequently (up to every 1 h). Individuals were monitored for a period of 2 years on average, with some individuals being monitored for up to 10 years. New individuals were captured every winter over areas covering thousands of km^2 to avoid capturing individuals from the same groups. At the onset of the monitoring, as few as 6 individuals per year were monitored, but this number increased gradually to reach ≥65 individuals per year after 2013 (Appendix S1: Table S1).

Starting in 1994, the herd was monitored every year (except 1999) during the rut (end of October) to classify individuals according to their sex and age classes (Taillon et al., 2016). Each year, an average of 3220 ± 273 (SD) individuals were classified, allowing the estimation of annual calf/cow (≥2 years old females) ratios. We used these calf/cow ratios as an index of recruitment, as commonly used for caribou management (DeCesare et al., 2012; Taillon et al., 2016).

Data preparation

We deleted GPS locations with dilution of precision values >10 and manually investigated all movements faster than 5 km/h. For each individual-year, we used net squared displacement to determine the start and end dates of spring migrations (Bunnefeld et al., 2011). If the start and end date were impossible to determine due to a collar failure or mortality, we omitted the data from this individual during that year. In total, we kept 197,759 GPS locations belonging to 811 individual spring migrations.

Mapping of migration routes

We delineated the annual migration routes used by individuals by connecting successive GPS locations (Figure 1A,B) and adding a 2112 m buffer on each side (total width of 4224 m; Figure 1C). This value was the average distance (SD = 1681 m) traveled by female caribou between two successive 13 h-GPS locations, that is, the most common time interval in our dataset. Each year, we grouped individual migration routes into population migration routes, representing the sum of migration routes used by all monitored individuals of the herd during a given year (Figure 1D). As GPS locations were collected more frequently after 2010, the delineation of population migration routes tended to be more precise after 2010.

Habitat selection during spring migrations

We performed resource selection functions (RSFs; Manly et al., 2002) by comparing the resources used by female caribou to the resources available to them. We investigated habitat selection at the population scale by drawing 5000 locations randomly within each annual population migration route and considering these as “used” locations (Figure 1E). To estimate availability, we built the smallest orthogonal polygon comprising the population migration route for that year, which we clipped to the area of northern Québec, that is, the Ungava peninsula (Figure 1F). We then drew 50,000 locations randomly within that polygon, which represented resource availability (Figure 1G). This sampling design differs from standard RSFs for a few reasons: (1) the movements of caribou during spring migrations are rapid and highly directional, meaning that typical approaches for delineating seasonal home ranges (e.g., minimum convex polygons) perform poorly, (2) we knew from data exploration that caribou used the entire Ungava peninsula during spring migrations, justifying analyses at a very broad scale, (3) the resolution of many environmental variables was low, for example, 32.5 km^2 for snow depth

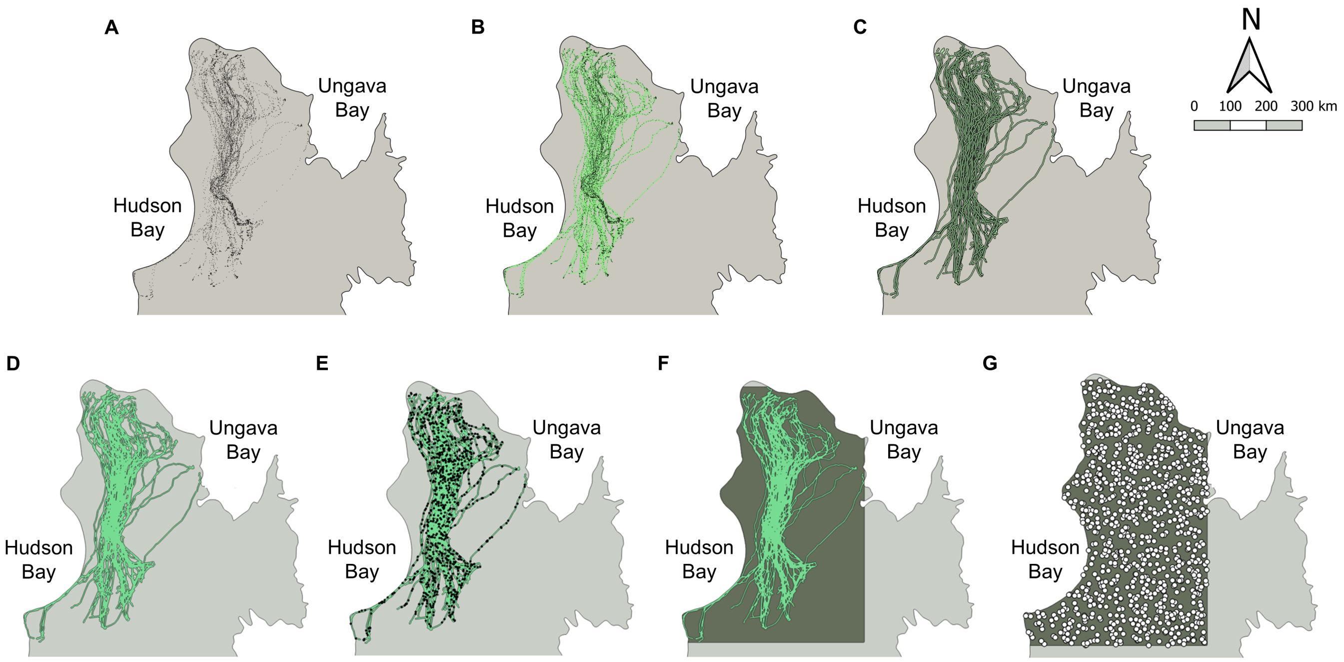

FIGURE 1 Sampling design used to study habitat selection during spring migrations by the Rivière-aux-Feuilles caribou herd in northern Québec, Canada. This example is for 2019; the same approach was used each year. (A) GPS locations of 72 caribou are represented by black dots; (B) individual migration routes are obtained by connecting the dots with lines); (C) individual migration routes are buffered by 2112 m on each side; (D) individual migration routes are grouped together to produce a population migration route; (E) random sampling of 5000 points across the population migration route, representing the “used” locations (black circles); (F) minimal orthogonal polygon encompassing the population migration route, then clipped to the area of northern Québec (gray area); (G) random sampling of 50,000 points in the clipped polygon, representing the “available” locations (white circles). This image shows a lower number of locations for increased visibility.

and precipitation, and (4) the variation in the number of individuals monitored each year and the variation in the frequency of relocations (5 days to 1 h) meant that we could not easily combine raw GPS locations in the same analysis. Under each location (used and available), we extracted the snow depth (in meters), precipitation (in kilograms per square meter), elevation (in meters), and land cover class (see below). We obtained estimates of snow depth and precipitation from the North American Regional Reanalysis (NARR) produced by the National Centers for Environmental Predictions at a 32.5-km^2 resolution (NOAA/OAR/ESRL PSL, Boulder, USA). We used model predictions for the month of May of each year, as they represented environmental conditions prevailing during spring migrations (Leclerc et al., 2021). Elevation came from a digital elevation model with a 100-m resolution. We extracted land cover information using the Végétation du Nord Québécois map (Leboeuf et al., 2018), which has a 3-ha resolution for waterbodies and 16 ha otherwise. This map includes 72 categories, which we combined into 7 classes meaningful for caribou ecology (Appendix S1: Table S2 for details): tundra, erect-shrub tundra, shrub tundra, forest, lichen heath, water, and other. We used shrub tundra as the reference category in RSF models.

We used logistic regression to compare environmental characteristics at used versus available locations in R using the *lme4* package (Bates et al., 2015). We generated multiple candidate RSF models which we compared using Akaike's information criterion (AIC; Burnham & Anderson, 2002; see Table 1) using the *MuMIn* package (Bartoń, 2024). We included a quadratic term for snow depth in all models to consider non-linear relationships, and we scaled (mean = 0, variance = 1) all quantitative variables to allow model convergence and facilitate interpretation. We included year as a random intercept in all models, and we assessed multicollinearity by measuring the variance inflation factor (VIF; Graham, 2003). Multicollinearity was low with VIF < 2.58.

Geographic position of migration routes and relationship to recruitment

We characterized the geographic position of population migration routes each year by calculating the mean longitude and mean variance of longitude of all individual migration routes in a given year. We used the mean variance of longitude as a proxy for the width of the population migration routes. We further determined the mean longitude at 58° N latitude, which approximately corresponds to the latitude crossed by caribou at the halfway mark of their spring migrations. We included these three metrics in a principal components analysis using the *prcomp* function in R, which we combined with a *k*-means cluster analysis (Lloyd, 1982) to explore variations in the geographic position of migration routes across years. We also used general additive models (GAMs) to explore temporal trends (i.e., year fitted with a spline function as the independent variable) in the mean longitude, mean variance of longitude, and mean longitude at 58° N. For the mean variance of longitude model, we also controlled for the number of females monitored. Finally, we evaluated if calf recruitment the following fall (indexed by the number of calf/100 adult females in the fall) was influenced by the geographic position of the spring population migration routes. We created 5 candidate linear models (see Table 2) and selected the best

TABLE 1 Candidate models of resource selection functions used to assess habitat selection along spring migration routes by female caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019.

Model	Covariates	*k*	LL	AIC	ΔAIC
Habitat	Erect-shrub tundra + forest + lichen heath + tundra + waterbodies + other	8	−427,929	855,874	19,599
Elevation	Elevation	3	−432,669	865,344	29,069
Weather	Precipitation + snow ^{2}	5	−422,280	844,570	8295
Habitat + elevation	Elevation + erect-shrub tundra + forest + lichen heath + tundra + waterbodies + other	9	−426,543	853,105	16,830
Habitat + weather	Precipitation + snow ^{2} + erect-shrub tundra + forest + lichen heath + tundra + waterbodies + other	11	−419,145	838,313	2038
Elevation + weather	Precipitation + snow ^{2} + elevation	6	−420,346	840,705	4430
Global	Precipitation + snow^2 + elevation + erect-shrub tundra + forest + lichen heath + tundra + waterbodies + other	12	−418,126	836,275	0

Note: Each model is shown with the number of parameters (*k*), log-likelihood (LL), Akaike's information criterion (AIC) value, and AIC difference from the top model (ΔAIC). All models used shrub tundra as the reference category and included year as a random effect.

model based on AIC (Burnham & Anderson, 2002). We ran all spatial analyses in QGIS 3.22.1 and statistical analyses in R v.4.3.3 (R Core Team, 2024).

RESULTS

Mapping of migration routes

We mapped the individual migration routes ($n = 811$ routes used by 304 individuals) and population migration routes ($n = 26$) of the Rivière-aux-Feuilles caribou herd from 1994 to 2019. By overlapping all spring migration routes over a period of 26 years, we found that nearly all areas of northern Québec had been used by caribou during spring migrations. A visual examination of migration routes through time revealed high variation in the location and width of migration routes at the population level (Appendix S1: Figure S1).

Habitat selection during spring migrations

The best-fit model included all variables, that is, the "global" model (Table 1). Caribou selected areas with less precipitation and lower elevation (Table 3), but with deeper snow (Figure 2). Caribou selected more strongly erect-shrub tundra and waterbodies than they did shrub tundra, the reference category (Table 3), and they avoided forest and lichen heath.

Geographic position of migration routes and its relationship to recruitment

Three migration patterns emerged from the principal components analysis (Figure 3). Migration routes in Pattern 1 were located to the west, along the Hudson Bay coast, with relatively diffuse (i.e., widespread) extremities, but closely grouped movements at the halfway mark of 58° N. Migration routes in Pattern 3 were less tightly grouped and located more easterly, towards the center of the Ungava Peninsula. Migration routes in Pattern 2 were intermediate between patterns 1 and 3. The GAM models revealed that the mean longitude of migration routes varied across years (estimated degrees of freedom = 4.63, $p < 0.001$; Figure 4A), from 75° W in the late 1990s to 74° W in the early 2000s and then back to 75° W around 2010 (a full degree of longitude at latitude 58° N represents approximately 60 km). We also observed that the mean longitude at 58° N (estimated degree of freedom = 1, $p = 0.003$; Figure 4B) decreased through time, whereas the mean variance of longitude (estimated degree of freedom = 1, $p = 0.08$; Figure 4B) showed a non-significant declining trend with time (Figure 4C). The model with the lowest AIC that assess the effect of the geographic position of population migration routes on calf/cow ratios in the following fall was the null model (Table 2), indicating that the observed changes in migration route locations had no measurable effect on calf recruitment.

DISCUSSION

Migratory caribou perform one of the longest terrestrial migrations in the animal kingdom, requiring the use of energy reserves to access foraging opportunities and to safely reprieve from predators, with consequences on fitness of individuals and ultimately, population dynamics (Eggeman et al., 2016; Fancy & White, 1987; Heard et al., 1996). In line with our predictions, we found that caribou selected areas receiving less precipitation and areas located at lower elevation. Contrary to our prediction, however, caribou selected deeper snow, and although we found that the location of population migration routes varied throughout a 26-year period and covered almost the entirety of northern Québec, these changes had no perceived influence on calf recruitment.

TABLE 2 Candidate models used to evaluate the link between the geographic position of migration routes and recruitment the following fall (i.e., about 6 months later), for caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019.

Model	Covariates	k	LL	AIC	ΔAIC
1	Mean variance of longitude × no. females	4	−7.128	27.6	6.4
2	Mean longitude	2	−8.282	23.8	2.6
3	Mean longitude at 58°	2	−7.693	22.6	1.4
4	Mean variance of longitude	2	−7.141	21.5	0.3
5	Null model	1	−8.315	21.2	0

Note: Each model is shown with the number of parameters (k), log-likelihood (LL), Akaike's information criterion (AIC) value, and AIC difference from the top model (ΔAIC).

We observed high variability in the location of spring migration routes at both the individual and population levels, with broad-scale changes happening as fast as from one year to the next (Appendix S1: Figure S1; see also Leclerc et al., 2021). A post hoc visualization of the spring migration routes for females with ≥9 years of monitoring (Appendix S1: Figure S2) showed that individuals modified their migration routes throughout their life, meaning that variations were not only driven by individual differences (Leclerc et al., 2016). Caribou could change the location or the speed of their migration in response to extrinsic factors, such as meteorological conditions, which can vary from year to year (Cameron et al., 2021; Leclerc et al., 2021). At broader temporal and spatial scales, tundra vegetation can be depleted locally by browsing and trampling from prior years, especially lichens which take decades to recover (Heggenes et al., 2017). This could also explain changes in the location of migration routes over time. Finally, Le Corre et al. (2020) showed that the location of wintering grounds varied according to weather conditions and population size. This difference in the starting point of migrations could also have influenced the location of spring migration routes; however, this effect was not directly measured in this study.

In the early 2000s, at peak population abundance, migration routes were located close to the center of the Ungava Peninsula and were less tightly grouped (Pattern 3, Figure 3). The decline in population size towards the end of the study period coincided with a general movement of migration routes towards the Hudson Bay, together with closely grouped movements (Pattern 1, Figure 3). Albeit not statistically significant ($p = 0.08$), we observed a reduction in the width of migration routes over time that could be explained by reduced space use and range size during periods of lower population size and intraspecific competition (Couturier et al., 2009; Le Corre et al., 2020). This result is in line with the abundance–occupancy relationship, which states that a lower number of individuals should distribute over

TABLE 3 Parameter estimates (β) and 95% CIs of variables included in the best-fit model used to assess habitat selection along spring migration routes by caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019.

		95% CI	
Variables	**β**	**Lower**	**Upper**
Precipitation	−0.129	−0.140	−0.118
Elevation	−0.163	−0.170	−0.156
Snow^2	0.037	0.031	0.043
Snow	0.510	0.501	0.518
Tundra	0.001	−0.022	0.024
Erect-shrub tundra	0.137	0.117	0.158
Forest	−0.348	−0.377	−0.320
Lichen heath	−0.420	−0.459	−0.381
Waterbodies	0.130	0.109	0.151
Other	−0.657	−0.694	−0.620

Note: The land cover variables (Tundra [availability = 17.1%, use = 19.8%], Erect-shrub tundra [availability = 23.0%, use = 31.1%], Forest [availability = 17.3%, use = 7.9%], Lichen heath [availability = 4.9%, use = 2.6%], Waterbodies [availability = 22.2%, use = 24.5%], and Other [availability = 5.5%, use = 3.0%]) are interpreted in relation to shrub tundra [availability = 10.1%, use = 11.2%], the reference category.

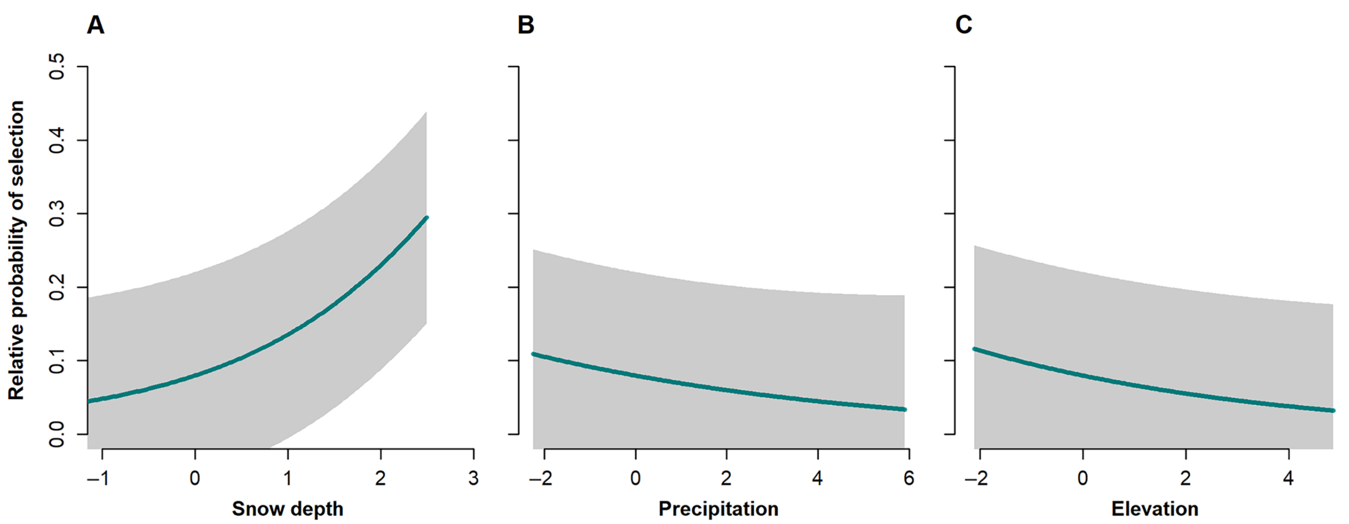

FIGURE 2 Effect of (A) snow depth, (B) precipitation, and (C) elevation on the relative probability of selection along spring migration routes used by female caribou from the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019. Independent variables were standardized (mean = 0, variance = 1) for ease of interpretation and model convergence.

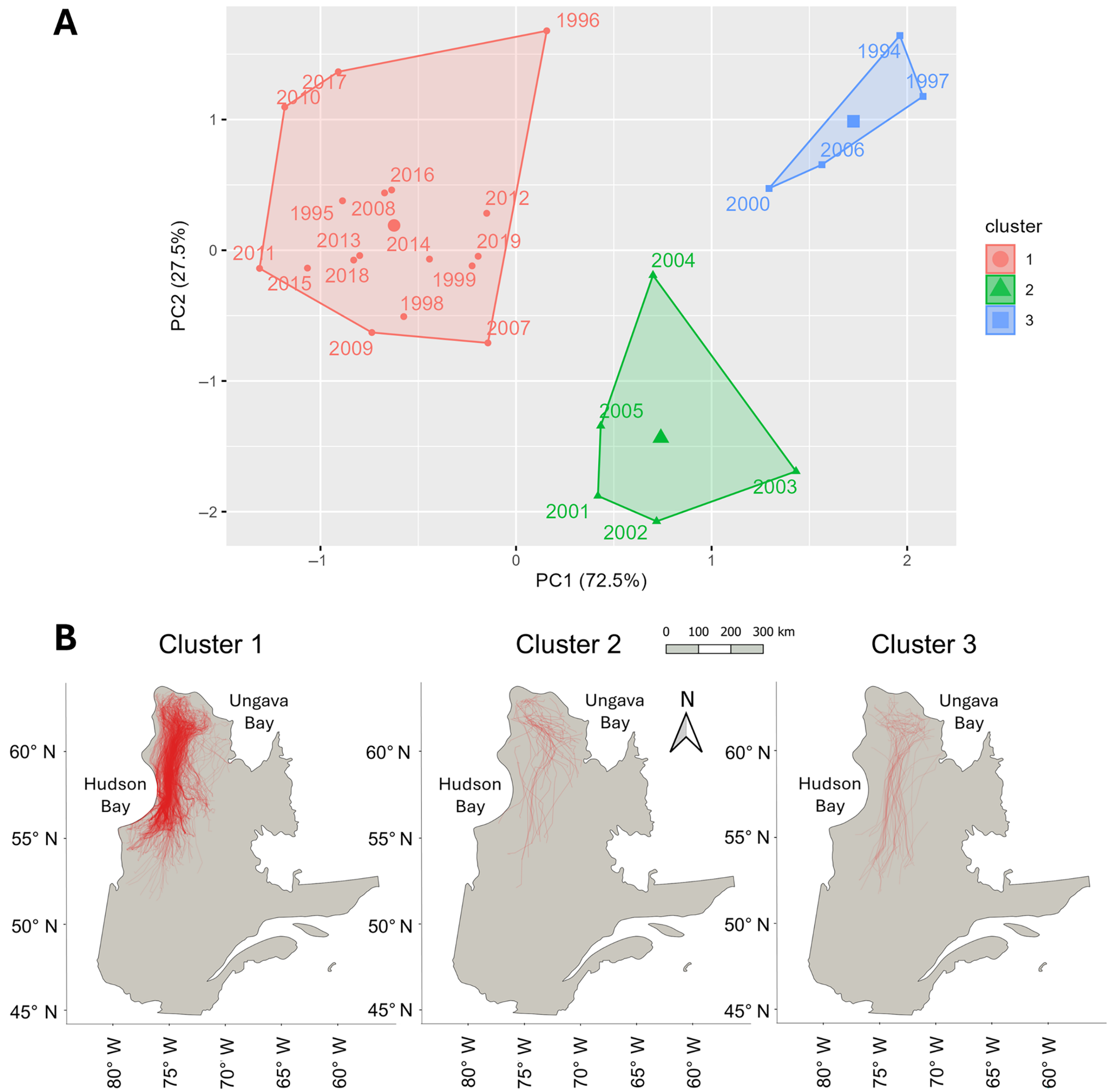

FIGURE 3 (A) Principal components and (B) cluster analyses used to identify similarity in patterns of spring migrations by female caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019. We compared migration corridor patterns based on their mean longitude and mean variance of longitude. The analysis suggested three clusters: Pattern 1 groups migration routes located along the Hudson Bay coast that are characterized by widespread extremities and closely grouped movements at intermediate latitudes; Pattern 2 groups migration routes with intermediate location and width; Pattern 3 groups migration routes located closer to the center of the Ungava Peninsula that are characterized by less tightly grouped movements.

a smaller area (Gaston et al., 2000). Population size likely influenced both the location and width of caribou migration routes (Joly et al., 2021), but that effect was likely confounded with changes in sampling in our analyses (see *Limits*).

During spring migrations, caribou avoided areas receiving more precipitation, likely due to the negative impacts of rain and snow on visibility. For example, Richard et al. (2014) showed that mountain goats (*Oreamnos americanus*) traveled shorter distances in areas with more snow precipitation. Contrary to our prediction, caribou selected areas with deeper snow and avoided shallow snow or snow-free ground, presumably because these areas are

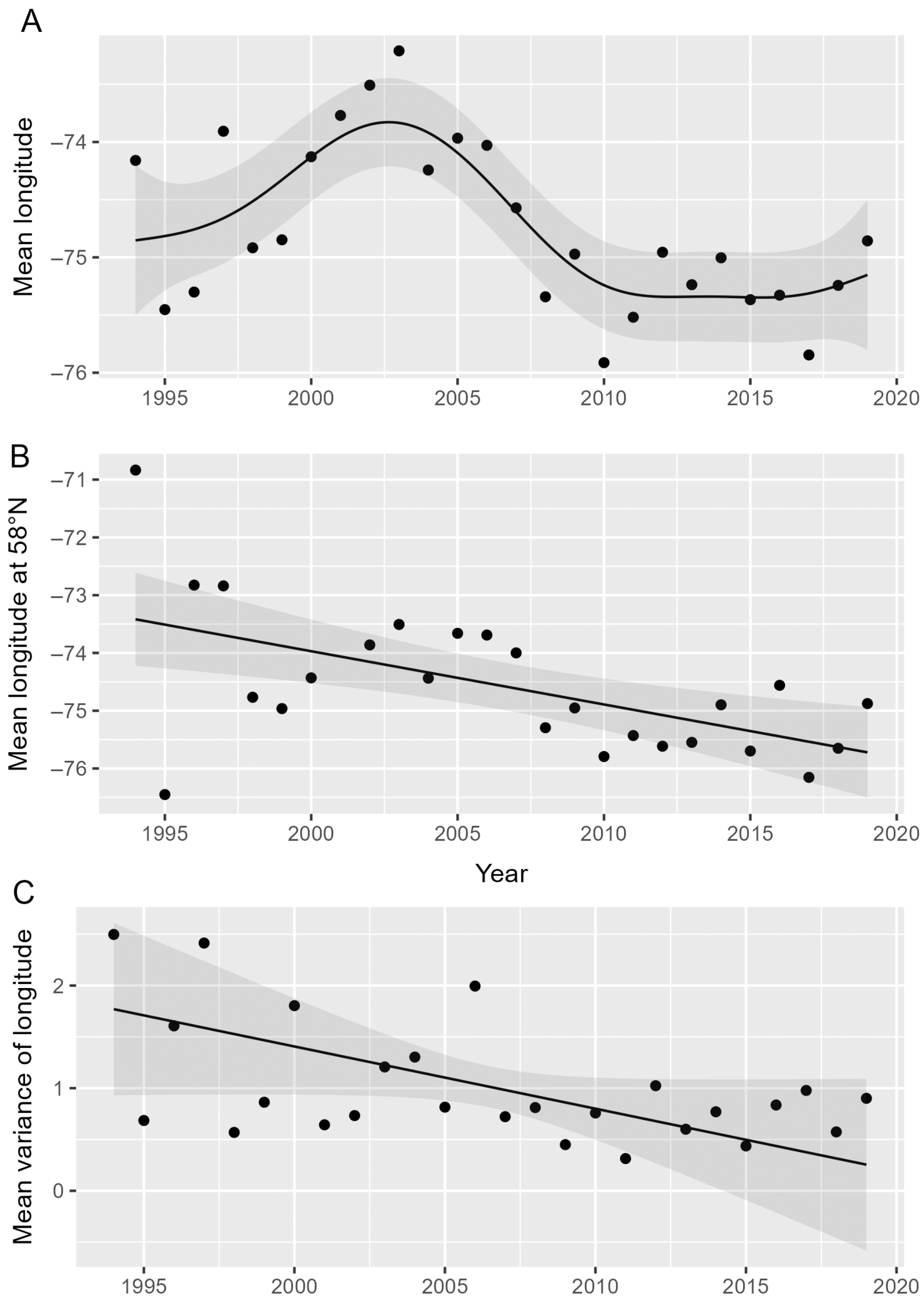

FIGURE 4 Results of the general additive models (GAMs) exploring temporal trends in the geographic position of migration routes used by female caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada, 1994–2019. The results showed (A) temporal variation in the mean longitude, (B) a decrease in the mean longitude at 58° N latitude, and (C) a negative trend ($p = 0.08$) in the mean variance of longitude (a proxy for corridor width).

typically devoid of vegetation (e.g., boulder fields). Locomotion energy expenditures are higher in deep snow, but caribou legs are well adapted to walking on snow (Fancy & White, 1985, 1987), and caribou are able to find food by "cratering" through the snow. In addition, caribou may reduce the costs of locomotion by using trails of compacted snow left by the individuals preceding them (Fancy & White, 1986). Wolf predation could also influence caribou habitat selection as evidence shows that wolves migrate with caribou in spring and autumn (Michelot et al., 2024). Contrary to moose which have a high foot load, caribou foot load is similar to wolves (Telfer & Kelsall, 1984) and by selecting deeper snow during migration, caribou may reduce encounter rates with wolves and potentially reduce predation risk. Our results also showed that caribou avoided high elevation, possibly to lower the energy costs of traveling across strong altitudinal gradients (Fullman et al., 2017; White & Yousef, 1978). This would be in line with results by Plante et al. (2017) and Leclerc et al. (2021), but contrary to results by Yannic et al. (2014) who suggested that elevation was a poor predictor of habitat suitability for three ecotypes of caribou in northern Québec.

Similarly to Fullman et al. (2017) who studied the migrations of barren-ground caribou in northwestern Alaska, we found that caribou in northern Québec avoided forested areas during spring migrations. Contrary to our prediction, our results showed that lichen heath were avoided more strongly during spring migration than shrub tundra, the reference category. This is surprising because lichen heath are often considered a habitat with abundant food resources for caribou. Caribou could compensate for lower energy intake by choosing instead to move through easy terrain, thereby limiting the costs of locomotion. Alternatively, it is possible that food resources are selected at a finer spatial scale than that of migration corridors. For example, Sawyer and Kauffman (2011) showed that stopover sites, in mule deer, presented higher forage quality than movement corridors. Finally, waterbodies and erect-shrub tundra were selected more strongly than shrub tundra. Frozen waterbodies can be an efficient way to travel and Leblond et al. (2016) showed that caribou selected frozen waterbodies during spring migration. They also showed that caribou had higher movement rates and directionality while moving on frozen waterbodies.

Limits

We used a dataset of 304 individuals monitored over 26 years, with sometimes long intervals between successive GPS locations. While time intervals were shorter towards the end of the study period (2011–2019), we used the whole dataset to maximize the information on variations in caribou migration routes over time. A post hoc habitat selection analysis isolating data before versus after 2010 showed that the best-fit model and biological interpretation was similar for the isolated periods (1994–2010 vs. 2011–2019) compared to the complete study period 1994–2019 (Appendix S1: Table S3), suggesting that our results were robust to the variable GPS interval schedules. The number of individuals monitored each year also varied throughout the study period (from 10 to more than 70; Appendix S1: Table S1). Again, this means that the migration routes we mapped in later years were likely more representative of the whole population compared to pre-1999. We did control for sample size in the analyses on the geographic position of migration routes, ensuring robust estimates for the explanatory variables of interest. Mapping of migration corridors of large ungulates should therefore be planned using large sample size with frequent GPS relocations. Integrating finer resolution environmental data as well as metrics describing characteristics of snow (e.g., compactness and wetness) in future studies on caribou migrations could provide better estimations of the costs of locomotion. Finally, although we tested for the effect of the geographic location of migration routes on calf recruitment, we did not have access to individual vital rates like reproductive success or body condition. Such information could help understand the effects of specific migration behaviors on fitness and ultimately, demography.

Caribou migrations in a changing world

Observed variations in the location of spring migration routes used by caribou suggest that caribou are able to adjust their behavior to environmental conditions. This behavioral plasticity could be key for the species' ability to adjust to fast-changing environmental and climatic conditions. The Arctic could warm by 3–10°C in the next decades (Overland et al., 2019), and precipitation patterns are already punctuated by more frequent extreme events (Bourque & Simonet, 2008; Ouranos, 2015). Such changes could modify the phenology of thawing and freezing of waterbodies (Brown & Duguay, 2011; Magnuson et al., 2000), hasten plant emergence and growth, and create mismatches between resource availability and the presence of caribou on their calving grounds and summer ranges (Joly et al., 2021; Post & Forchhammer, 2008). Sharma et al. (2009) predicted that, in response to climate change, the Rivière-aux-Feuilles caribou herd could benefit from an increase in size of suitable range, which could alter its migration patterns. Moreover, the current migration routes of caribou are relatively free of human infrastructure (Plante et al., 2020), but the Ungava peninsula is increasingly being targeted for industrial development and hydroelectricity production. Land managers will need to consider landscape connectivity and the critical importance of maintaining long-distance migrations in the future to connect calving grounds located in the tundra with wintering grounds located in the boreal forest (Boulanger et al., 2012).

Mapping the migration routes of the Rivière-aux-Feuilles caribou herd over 26 years contributed to a better understanding of caribou space use in a period of increasing interest for the exploitation of mineral and energetic resources (Berteaux, 2013). Wildlife managers now have access to a comprehensive list of environmental variables and their impacts on habitat selection during spring migrations. They can also visualize maps of population migration routes representing critical connections between seasonal habitats that should be maintained. Future work exploring caribou migration routes under various climate change scenarios could help predict future changes in migration and target areas for long-term protection. Such knowledge would be needed at a time when animal migrations are declining globally.

AUTHOR CONTRIBUTIONS

Conceptualization: All authors. *Data curation*: Cassandra Mac Hugh and Martin Leclerc. *Formal analysis*: Cassandra Mac Hugh and Martin Leclerc. *Funding acquisition*: Joëlle Taillon, Mathieu Leblond, and Steeve D. Côté. *Project administration*: Joëlle Taillon and Steeve D. Côté. *Writing—original draft preparation*: Cassandra Mac Hugh and Martin Leclerc. *Writing—review and editing*: All authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Leclerc et al., 2025) are available from Borealis: https://doi.org/10.5683/SP3/0ROESU.

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SUPPORTING INFORMATION

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

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