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Determinants of migration trajectory and movement rate in a long-distance terrestrial mammal

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Animal migrations occur in many taxa and are considered an adaptive response to spatial or temporal variations in resources. Human activities can influence the cost-benefit trade-offs of animal migrations, but evaluating the determinants of migration trajectory and movement rate in declining populations facing relatively low levels of human disturbance can provide new and valuable insights on the behavior of wildlife in natural environments. Here, we used an adapted version of path selection functions and quantified the effects of habitat type, topography, and weather, on 313 spring migrations by migratory caribou (*Rangifer tarandus*) in northern Québec, Canada, from 2011 to 2018. Our results showed that during spring migration, caribou selected tundra and avoided water bodies, forest, and higher elevation. Higher precipitation and deeper snow were linked to lower movement rates. Weather variables had a stronger effect on the migration trajectories and movement rates of females than males. Duration of caribou spring migration (mean of 48 days) and length (mean of 587 km) were similar in males and females, but females started (22 April) and ended (10 June) spring migrations ca. 6 days earlier than males. Caribou spring migration was influenced by habitat type, topography, and weather, but we also observed that caribou migrations were not spatially constrained. Better knowledge on where and when animals move between their winter and summer ranges can help inform management and land planning decisions. Our results could be used to model future migration trajectories and speed of caribou under different climate change scenarios.

Keywords: declining population, Eastern migratory caribou, movement, Nunavik, *Rangifer tarandus*, resource selection, Rivière-aux-Feuilles caribou herd

Migration is a behavior observed in many animal taxa, from small insects to large baleen whales (Dingle and Drake 2007; Sinclair et al. 2011). Animals can migrate over different time scales varying from daily (e.g., zooplankton) to seasonal migrations (e.g., wildebeest, *Connochaetes taurinus*), and can cover distances of up to thousands of kilometers, such as in the Arctic tern (*Sterna paradisaea*—Egevang et al. 2010) or humpback whale (*Megaptera novaeangliae*—Stevick et al. 2011). Although migrations can induce high energetic costs that potentially can reduce fitness (Lok et al. 2015), animal migrations are considered an adaptive response to spatial or temporal variations in resources and predation risk (Gauthreaux 1982; McKinnon et al. 2010; Avgar et al. 2014). Migrations can provide benefits such as reduction in predation risk and increased access to mates and high-quality forage (Fryxell and Sinclair 1988; McKinnon et al. 2010; Bischof et al. 2012; Middleton et al. 2018). There is, however, increasing evidence that human activities can influence the cost-benefit trade-offs of animal migrations, which has resulted in a general decline in animal migration occurrences and migratory populations worldwide (Sanderson et al. 2006; Wilcove and Wikelski 2008). Much research has been done to investigate how human activities (e.g., habitat modifications, creation of barriers such as highways and fences) can impede animal movements and migrations, and, ultimately, their demographic, ecological, and evolutionary impacts (Holdo et al. 2011; Bauer and Hoye 2014; Seidler et al. 2015; Turbek et al. 2018). We have, however, a poorer understanding of how climate related factors may affect terrestrial migratory populations. Studying migratory patterns of animals living in pristine environments could provide valuable insights about their natural behaviors.

Northern Québec, Canada, is a vast area with relatively few human disturbances (Sanderson et al. 2002). Migratory caribou (*Rangifer tarandus*) inhabit this region, where they display one of the longest terrestrial migrations in the animal kingdom (Joly et al. 2019). Migratory caribou migrate during the spring to reach calving grounds approximately 600 km away from wintering grounds, where females give birth to one calf mid-June, then move back to their wintering grounds during the fall (Le Corre et al. 2017). The onset of the spring migration usually begins when snow still is abundant, and caribou often travel > 40 km per day (Le Corre et al. 2017). Calving is believed to be synchronized with the annual peak in resource availability on calving grounds, and trophic mismatches caused by climate change have been observed elsewhere (Post and Forchhammer 2008), but not in northern Québec (Le Corre et al. 2017). Fall migrations generally are much more diffuse than spring migrations and include long pauses ("stopovers") during the rut or to forage (Le Corre et al. 2017). Although human disturbances are present on caribou wintering grounds, they are much scarcer during caribou spring migration and on the summer grounds (Plante et al. 2018).

A better understanding of the factors influencing caribou migration patterns in a region where human footprint is low would provide valuable insights to inform management decisions and recovery of this species. For instance, studying migratory trajectories in natural environments could inform about the potential impacts of climate change, and help identify critical areas for natural connectivity. Here, we tested the effect of habitat type, topography, and weather, on the trajectory and movement rate of caribou during spring migrations, using an adapted form of path selection functions. We hypothesized that caribou would minimize energetic costs of traveling during spring migration. Based on previous research on migratory caribou in this region and elsewhere in North America, we predicted that caribou would select for heathlands and tundra to migrate but would avoid water bodies and higher elevation (Table 1). We also predicted that caribou would reduce their movement rate when faced with harsher environmental conditions such as higher precipitation and deeper snow (Table 1).

Materials and Methods

Study area.—The study area encompassed ca. 300,000 km^2 in northern Québec, Canada (Fig. 1). The caribou population under study, the Rivière-aux-Feuilles migratory caribou population, has undergone a 68% decline, from ca. 628,000 to 199,000 individuals, between 2001 and 2016 (Couturier et al. 2004). The winter range of the Rivière-aux-Feuilles migratory caribou herd is located in the southern portion of their annual distribution and is dominated by black spruce (*Picea mariana*) stands with tamarack (*Larix laricina*), interspersed with low vegetation composed of shrubs and lichens (Latifovic and Pouliot 2005). The calving and summer ranges are located in the northern part of their annual distribution and mainly are covered by arctic tundra dominated by shrubs (*Salix* sp. and *Betula* sp.), grasses, herbaceous plants, and terrestrial lichens (Latifovic and Pouliot 2005). Elevation ranges from sea level to 1000 m. Mean annual temperature was −3.6°C and mean annual precipitations were 1077 mm, most of which felt as snow between October and March (Berteaux et al. 2018).

Animal capture.—Between 2011 and 2018, we captured male and female migratory caribou using a net-gun fired from a helicopter. We equipped them with GPS tracking collars (Vectronics Aerospace using Iridium or Globalstar networks) programmed to take a location every 12 or 13 h. We avoided collaring individuals moving together by spreading captures over several thousands km^2. All captured caribou were part of the monitoring program of the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) and the Caribou Ungava research program at Université Laval. Capture, handling, and monitoring of caribou followed ASM guidelines and were approved by the Canadian Council on Animal Care and the Animal Care Committees of Université Laval and MFFP (permit # 2011039).

GPS data processing.—We removed five locations with dilution of precision > 10 to increase spatial accuracy and manually investigated all animal movements faster than 5 km/h, which led us to remove seven additional locations (< 0.02% of the data set) that showed unusual movement trajectory and speed. Our cleaned GPS data set (n = 26,712 locations) had an average fix success rate of 97%. We assessed departure and arrival dates of spring migrations by looking at abrupt changes in caribou movement patterns. We characterized movements of caribou using First-Passage Time (FPT—Fauchald and Tveraa 2003), which summarizes the velocity and tortuosity of movement

Table 1.—Predicted effect of habitat and climate variables included in models assessing caribou trajectory and movement rate during spring migrations in northern Québec, Canada (2011–2018).

Prediction	Rationale	Source
Trajectory		
(+) Tundra	Open and flat terrain facilitates movement.	White and Yousef (1978)
(−) Water bodies	Lakes are avoided because they are energetically costly to cross and increase risks of drowning.	Miller and Gunn (1986), Leblond et al. (2016)
(−) Elevation	Rolling terrain increases energy expenditures.	White and Yousef (1978)
Movement rate		
(−) Precipitation	Harsh conditions impede movements.	Le Corre et al. (2017)
(−) Snow depth	Energetic costs of movements in snow increase with sinking depth.	Fancy and White (1987)

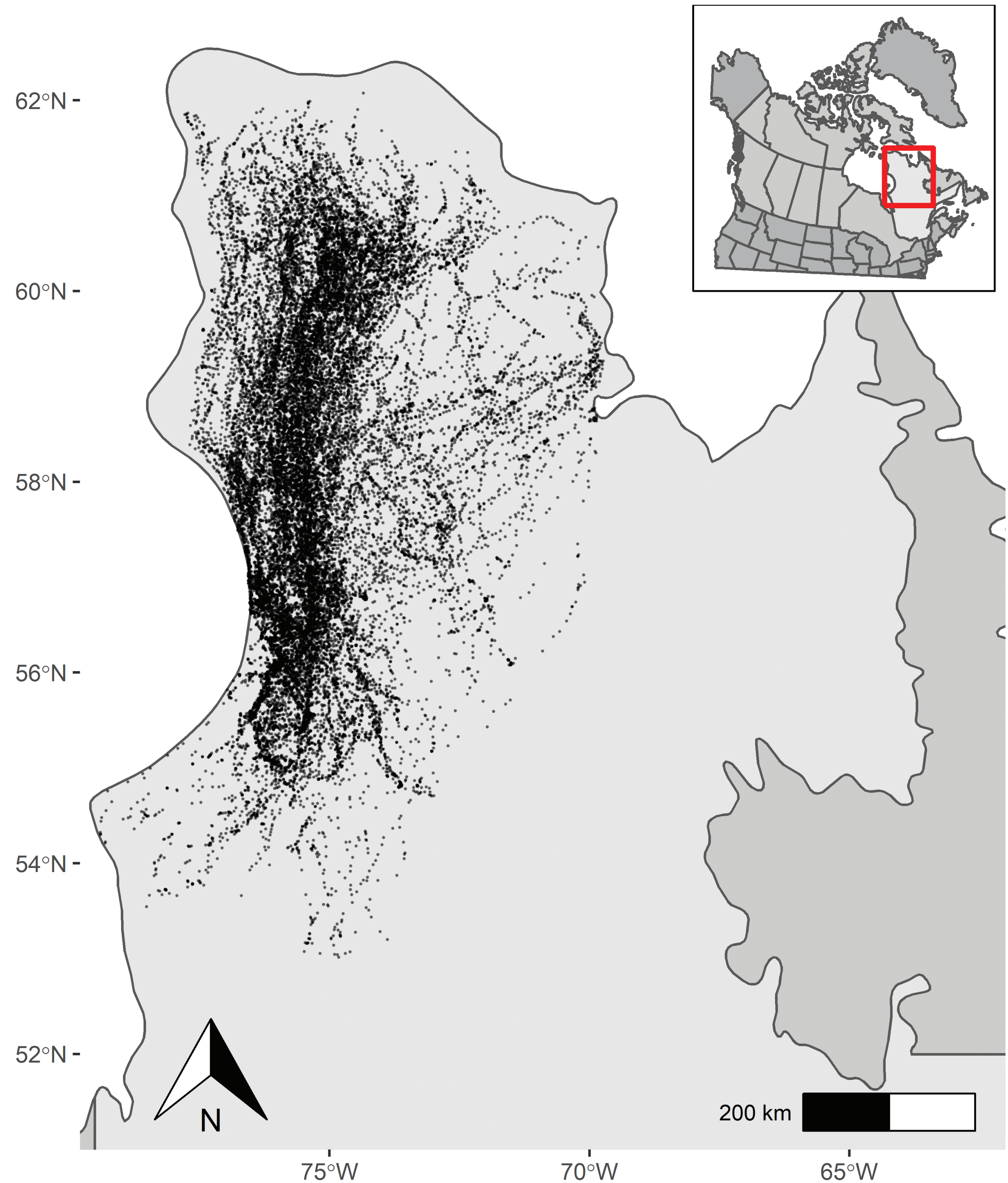

Fig. 1.—GPS locations (n = 26,712) of male (n = 48) and female (n = 143) caribou used to assess path selection during spring migrations (n = 313) in 2011–2018 in northern Québec, Canada.

along a path. FPT corresponds to the time needed by an individual to cross a circle of a given radius centered on each location of an animal path. Fast, directional long-distance movements that generally characterize caribou migrations result in lower FPT values. Based on work on the same caribou herd by Le Corre et al. (2014), we used a 25-km radius to compute FPT and applied the Lavielle segmentation process (Lavielle 2005) on FPT profiles to detect departure and arrival dates of spring migrations. See Le Corre et al. (2014) for further details.

Path selection functions.—To investigate the determinants of spring migration trajectory and movement rate by caribou, we undertook path selection functions (Zeller et al. 2012; Carvalho et al. 2016). Path selection functions compare environmental attributes along the path used by an animal to environmental attributes that could have been encountered along other available paths (Cushman and Lewis 2010; Zeller et al. 2016). Random paths usually are generated by randomly shifting and rotating used paths (Elliot et al. 2014; Carvalho et al. 2016). Here, however, we defined the random path by randomly reordering each step (i.e., a step is the vector connecting two consecutive GPS locations) composing the real observed path (Fig. 2; see also Pullinger and Johnson 2010). This new approach allowed us to compare the variables at observed locations along an animal path to locations along random paths that the animal could have taken between the same migration end points. Caribou paths were composed of 90 ± 22 (mean ± *SD*) steps and we characterized the real and random paths by extracting elevation, habitat types, and weather variables, at each inflexion point (each step). We extracted elevation from a digital elevation model with a 100-m resolution. We extracted habitat types from a vegetation map (Végétation du Nord Québécois 2018) provided by the MFFP. Minimum mapping unit size was 16 ha for polygons with vegetation and 3 ha for wetlands and water bodies. We divided habitat types into seven categories: tundra, erect shrub tundra, shrub tundra, heathlands, forest, water bodies, and other. We characterized used and available paths with daily variables of air temperature, precipitation (mainly snow; kg/m^2), snow depth (m), snow cover (%), and snowmelt (kg/m^2). We extracted all weather variables from a 32.5-km resolution raster obtained from the NCEP North American Regional Reanalysis (https://psl.noaa.gov). We estimated the movement rate (distance/time) of caribou for each step, for both real and random paths.

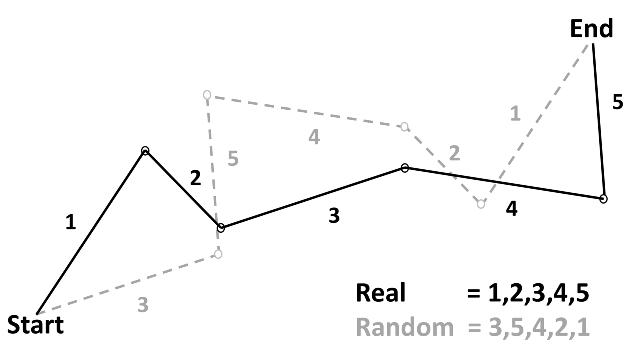

Fig. 2.—Design of the path selection function. We determined the available path (gray dotted line) by randomly reordering the vectors (each step between two consecutive locations) that composed a real migration path (black solid line). This approach allowed us to compare random migration paths that started from and ended in the same locations as the true migration paths. We characterized the path by extracting environmental variables at each inflexion point (black and gray dots). This illustration represents a simplified path; observed caribou paths were composed of 90 ± 22 (mean ± *SD*) steps on average.

Statistical analyses.—We first tested whether spring migration phenology differed between male and female caribou. We ran four linear mixed models with the lme4 package (Bates et al. 2015) in R 3.6.2 (R Core Team 2019) to determine the effect of sex on spring migration departure date (1), arrival date (2), duration (3), and length (4). We included year and caribou ID as random intercepts. We used a Likelihood ratio test to determine if the four linear mixed models with the effect of sex were significantly different than their respective null models with no dependent variable (random intercepts only).

To carry out the path selection function analysis, we ran conditional logistic regression models to compare real migration paths (coded 1) to random migration paths (coded 0). We also included year and caribou ID as random intercepts. Because the sampling unit was the migration path, we included caribou-year identity as the conditional stratum. Positive coefficients meant that an animal used such attributes more often than expected based on their availability, i.e., at inflexion points along the associated random paths. Because inference from use-available design in habitat selection studies can be influenced by the availability sample (Northrup et al. 2013), we ran sensitivity analyses. Based on the results of sensitivity analyses, we undertook the final analyses with a ratio of 1 used path compared to 100 random paths simultaneously, which was well above the threshold where the coefficients for all covariates started to stabilize (Supplementary Data SD1).

For the path selection function analysis, we carried out model selection (Burnham and Anderson 2002) and evaluated different candidate models using the Bayesian Information Criterion (BIC; Table 2). Models were constructed hierarchically and were composed of elevation, weather variables, habitat types (using shrub tundra as the reference category), and their interaction with the movement rate of the animals. We included interactions with movement rate to determine if elevation, weather, and habitat type influenced the probability of observing a high- or low-speed movement trajectory. We ran conditional logistic regressions for each sex separately and we validated the best-supported models using *k*-fold cross-validation following Johnson et al. (2006). Multicollinearity was low with all VIF < 1.5 (Graham 2003). We carried out all data processing and statistical analyses in R 3.6.2 (R Core Team 2019).

Results

Between 2011 and 2018, we monitored 48 male and 143 female migratory caribou and analyzed 313 spring migrations (males = 65, females = 248). Likelihood ratio tests revealed no significant differences between male and female spring migration duration (mean = 48.3 days, $\chi^2 = 0.22$, $P = 0.6$) or migration length (mean = 587 km, $\chi^2 = 0.23$, $P = 0.6$). Departure ($\chi^2 = 18.3$, $P < 0.001$) and arrival ($\chi^2 = 22.3$, $P < 0.001$) dates of spring migrations were earlier for females than males. Average female spring migration departure and arrival were on Julian dates 111.8 (22 April) and 161.3 (10 June), respectively, while average spring migration departure and arrival were, respectively, 5.7 and 6.6 days later for males.

The best-supported path selection function model for both females and males was the complete model (Table 2). According to the ΔBIC values of each model (Table 2) and β coefficients (Table 3), we observed that female path selection was influenced by (in decreasing order of importance) habitat types, weather, and elevation, whereas male path selection was influenced by habitat types, elevation, and weather. Movement rate was included in the best-supported models for both sexes,

Table 2.—Candidate models assessing habitat selection during spring migration of male (n = 48) and female (n = 143) caribou in northern Québec, Canada, between 2011 and 2018. Models are listed with their fixed effects (covariates), log likelihood (LL), differences in Bayesian Information Criterion (BIC) in relation to the best-supported model (ΔBIC), and model weight (w_i). All models were tested with Year and Caribou ID as random intercepts. Interactions are represented by the symbol × and the covariate "Speed" is the movement rate (km/h) of a caribou between two consecutive GPS locations.

Model	Covariates included	Male			Female		
		LL	ΔBIC	w_i	LL	ΔBIC	w_i
1	None	−43,693	2,095	0	−198,928	8,472	0
2	Elevation	−43,500	1,723	0	−198,906	8,443	0
3	Temperature + Precipitation + Snow depth + Snow cover + Snowmelt	−43,590	1,955	0	−198,507	7,703	0
4[a]	Erect shrub tundra + Heathlands + Forest + Water + Tundra + Other	−43,001	790	0	−195,689	2,083	0
5	Model 2 + Model 3	−43,389	1,568	0	−198,491	7,687	0
6	Model 2 + Model 4	−42,805	413	0	−195,616	1,951	0
7	Model 3 + Model 4	−42,808	470	0	−195,072	920	0
8	Model 2 + Model 3 + Model 4	−42,590	47	0	−194,969	729	0
9	Speed × Model 2	−43,465	1,680	0	−198,900	8,460	0
10	Speed × Model 3	−43,557	1,968	0	−198,303	7,383	0
11	Speed × Model 4	−42,964	808	0	−195,451	1,708	0
12	Speed × Model 5	−43,321	1,523	0	−198,278	7,361	0
13	Speed × Model 6	−42,738	383	0	−195,368	1,572	0
14	Speed × Model 7	−42,732	476	0	−194,623	198	0
15	Speed × Model 8	−42,481	0	1	−194,509	0	1

[a] Reference category = shrub tundra.

Table 3.—Coefficients (β) and 95% confidence intervals (*CI*s) of the best-supported conditional logistic regression model assessing path selection during spring migration for male (n = 48) and female (n = 143) caribou in northern Québec, Canada, between 2011 and 2018. Numbers in bold represent covariates for which *CI*s do not overlap 0. Interactions are represented by the symbol × and the covariate "Speed" is the movement rate (km/h) of a caribou between two consecutive GPS locations.

Covariates	Male			Female		
	β	95% *CI*		β	95% *CI*	
		Lower	Upper		Lower	Upper
Speed	**−5.125**	**−8.658**	**−1.592**	**5.244**	**3.280**	**7.209**
Elevation	**−0.006**	**−0.007**	**−0.006**	**−0.001**	**−0.002**	**−0.001**
Air temperature	**−0.065**	**−0.075**	**−0.055**	**−0.024**	**−0.029**	**−0.019**
Precipitation	**0.043**	**0.025**	**0.061**	**0.083**	**0.072**	**0.093**
Snow depth	**−2.565**	**−3.597**	**−1.533**	**−0.551**	**−0.865**	**−0.238**
Snow cover	**0.816**	**0.551**	**1.081**	**0.560**	**0.473**	**0.648**
Snowmelt	0.037	−0.046	0.120	**−0.125**	**−0.170**	**−0.081**
Erect shrub tundra	**0.278**	**0.153**	**0.403**	**0.681**	**0.617**	**0.744**
Heathlands	−0.011	−0.169	0.146	**0.122**	**0.032**	**0.212**
Forest	**−1.275**	**−1.443**	**−1.108**	**−0.796**	**−0.892**	**−0.701**
Other	**−0.333**	**−0.527**	**−0.140**	**0.445**	**0.338**	**0.553**
Water	**−2.036**	**−2.241**	**−1.831**	**−1.519**	**−1.617**	**−1.422**
Tundra	**0.342**	**0.152**	**0.532**	**1.163**	**1.078**	**1.247**
Speed × Elevation	**0.003**	**0.002**	**0.004**	−0.001	−0.001	0.000
Speed × Air temperature	**0.016**	**0.003**	**0.028**	**−0.018**	**−0.025**	**−0.011**
Speed × Precipitation	**−0.101**	**−0.131**	**−0.071**	**−0.139**	**−0.156**	**−0.121**
Speed × Snow depth	0.104	−1.295	1.504	**−0.489**	**−0.946**	**−0.033**
Speed × Snow cover	−0.137	−0.481	0.207	**−0.199**	**−0.314**	**−0.084**
Speed × Snowmelt	0.031	−0.069	0.132	**0.206**	**0.154**	**0.258**
Speed × Erect shrub tundra	0.041	−0.134	0.216	**−0.244**	**−0.330**	**−0.158**
Speed × Heathlands	**0.253**	**0.050**	**0.457**	**0.315**	**0.204**	**0.425**
Speed × Forest	**0.508**	**0.307**	**0.709**	**0.354**	**0.239**	**0.468**
Speed × Other	**0.295**	**0.049**	**0.541**	−0.106	−0.249	0.038
Speed × Water	**0.857**	**0.635**	**1.080**	**0.560**	**0.451**	**0.668**
Speed × Tundra	0.184	−0.076	0.443	**−0.559**	**−0.683**	**−0.435**

but our results suggest that the interaction between movement rate and the other covariates had stronger support for females (Table 2, model 8, ΔBIC = 729; Table 3) than for males (Table 2, model 8, ΔBIC = 47; Table 3).

Compared to associated random trajectories, female caribou selected lower elevation, with higher snow cover, lighter snowmelt, and thinner snow depth (Table 3; Fig. 3). The relative probability of selection of high-speed steps by female caribou

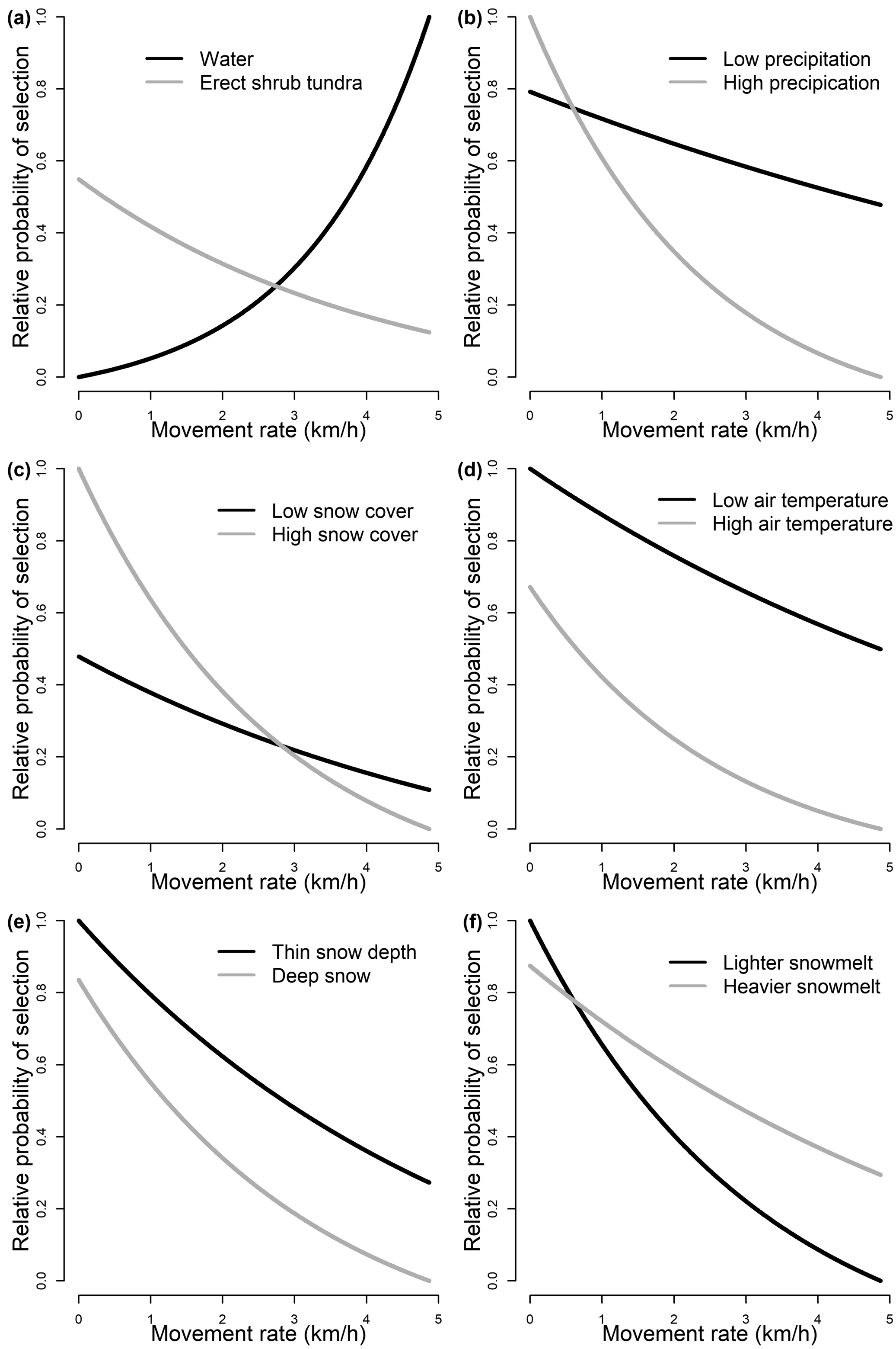

Fig. 3.—Results of the best-supported conditional logistic regression model describing spring migration path selection by female caribou in northern Québec, Canada, from 2011 to 2018. Predictions for weather variables were obtained in erect shrub tundra. Low and high values correspond to the 15th and 85th percentiles observed in the data set, respectively.

was higher at lower air temperature and lower precipitation (Fig. 3). Finally, female caribou selected tundra and erect shrub tundra more strongly than shrub tundra (i.e., the reference category) and females avoided forests and water bodies (Table 3), but the relative probability of selection of (frozen) water bodies increased with increasing movement rate of the animal (Fig. 3). Male selection of spring migration trajectories was similar to females but was not influenced by snowmelt. The interactions between movement rate and weather variables also had less support (Table 3). The selection of high-speed steps by male caribou was more likely on water bodies and at lower precipitation (Fig. 4). The best-supported models for both sexes were robust, with *K*-fold cross-validation of 0.97 ± 0.01 (mean ± *SD*) and 0.91 ± 0.04 for females and males, respectively.

Discussion

Using an adapted version of path selection functions, we investigated the effect of habitat types, topography, and weather on spring migration trajectory and movement rate of caribou in northern Québec, Canada. In accordance with our predictions, we found that caribou selected tundra and avoided water bodies and higher elevation during spring migrations. Harsher environmental conditions, namely deeper snow depth and higher precipitations, were linked to slower migrations, as predicted. We also showed that weather had a stronger effect on female migration trajectory and speed than for males. Finally, our results showed that the duration (ca. 48 days) and length (mean of 587 km) of the caribou spring migration were similar for males and females, but that females started (22 April) and ended (10 June) their spring migration about 6 days earlier than males.

In an environment characterized by very low human disturbance, we showed that environmental conditions shaped the migratory behaviors of caribou during spring. With their wide hooves, caribou are well-adapted to snowy environments and during spring migration both males and females selected areas with more snow cover. We found, however, that caribou avoided deep snow during migration, probably due to the higher energetic costs of traveling in deeper snow (Fancy and White 1987). We also showed that environmental conditions seemed to affect females more strongly than males. We hypothesize that female caribou may need to adjust their migration timing more precisely than males to match environmental cues. Indeed, while both males and females have a protein-deficient diet during winter, female energetic demands are higher than for males during the last stage of gestation, which coincides with spring migration (Chan-McLeod et al. 1994; Parker et al. 2005; Barboza and Parker 2008). Snow-covered environments during spring migrations prevent caribou from accessing fresh and newly grown vegetation. Females therefore might seek to adjust their spring migration speed and arrival on calving grounds with vegetation green-up (Post and Forchhammer 2008). We argue that snowmelt is a key environmental cue that occurs before green-up and we showed that the relative probability of selection of high-speed trajectory by females was higher

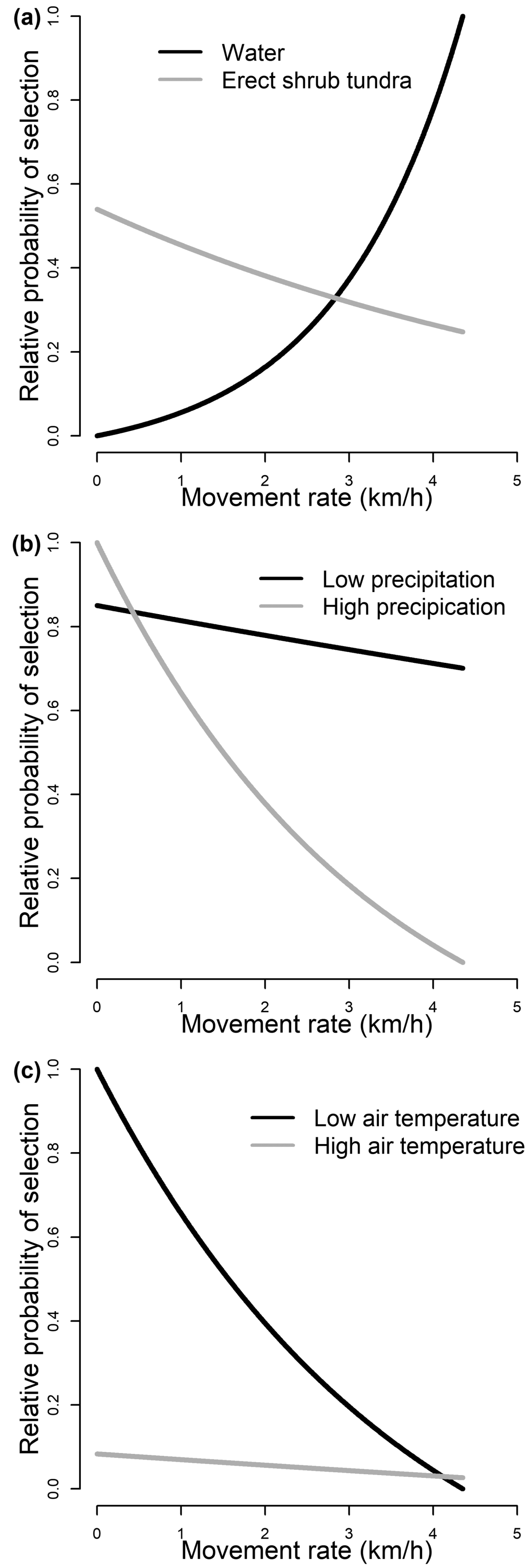

Fig. 4.—Predictions of the best-supported conditional logistic regression model describing spring migration path selection by male caribou in northern Québec, Canada, from 2011 to 2018. Predictions for weather variables were obtained in erect shrub tundra. Low and high values correspond to the 15th and 85th percentiles observed in the data set, respectively.

with increasing snowmelt (Fig. 3f). We hypothesize that females increase movement rates when snow is melting to reach calving grounds quicker and avoid missing the vegetation green-up, or to benefit from it earlier (Laforge et al. 2021). Alternatively, females also could increase movement rates when snow is melting to reach better snow conditions and avoid walking in melting snow (Laforge et al. 2021), which is energetically costlier (Shepard et al. 2013). Our results also showed that high-speed trajectory was unlikely when precipitation (mainly snow) was higher (Fig. 3b). Many studies have investigated the effects of precipitation on migration phenology in mammals and birds (Pettit and O'Keefe 2017; Haest et al. 2019), but few have looked at how precipitations influenced migration speed *en route*. During caribou spring migrations, precipitation falls mostly as snow, which may reduce visibility and limit individual's ability to navigate effectively and increase energetic costs of traveling (Fancy and White 1987; Shepard et al. 2013).

Habitat types and elevation were not used randomly by caribou during their migration. For instance, forested areas were avoided by caribou, similarly to another caribou population in northwestern Alaska (Fullman et al. 2017), potentially to facilitate travel and increase visibility to detect predators from further away. Open habitat types that provide increased visibility, such as tundra and erect shrub tundra, were selected by males and females, whereas water bodies were avoided. Although water bodies were avoided, the relative probability of selection of high-speed trajectory was higher when caribou were found on a water body compared to tundra or erect shrub tundra. Ultimately, we observed that the relative probability of selection of high-speed trajectory was at its highest when caribou were on a frozen water body (positive slope reaching y = 1 in Figs. 3a and 4a). The use of frozen water bodies therefore was a major determinant of caribou spring migration movement rates. Knowing that caribou rarely swam across water bodies and prefer to circumvent open water (Leblond et al. 2016), we expect spring migration speed and trajectory to be influenced by earlier lake ice melting caused by climate change (Dibike et al. 2012). Finally, our results showed that elevation was another important determinant of movement trajectory. Indeed, higher elevation was avoided by male and female caribou during spring migration, which was also observed in other caribou populations (Fullman et al. 2017) and in moose (Leblond et al. 2010), potentially due to the higher energetic costs of traveling (White and Yousef 1978).

Mapping the predictions from our best model (Supplementary Data SD2) confirmed that spring migrations of caribou in northern Québec were not heavily spatially constrained. This relative permeability of the landscape also was reflected in the raw GPS data on Fig. 1. Although caribou movements during spring migrations did not seem to be constrained, we observed that caribou sometimes used well-defined corridors to migrate such as in 2011 and 2013 (Figs. 5a and 5c). In other years, however, migration corridors were diffuse or even absent (Fig. 5d). Moreover, the location of spring migration corridors varied annually (Fig. 5). Caribou could use different migration corridors over time to access new resources or to adjust to the weather conditions they encounter during travel. Vegetation grows slowly in the Arctic, and past foraging as well as trampling by caribou could force them to displace their migration corridors to access better-quality or more abundant forage (Ferguson et al. 2001; Joly et al. 2010). We also hypothesize that caribou could use different migration corridors over time to reduce their predictability and potentially reduce predation risk. Indeed, searching for prey over vast landscapes such as northern Québec might be more costly for predators.

We found that females left the wintering grounds and arrived on calving grounds earlier than males. This result could be explained by the constraint that pregnant females have to reach calving sites in time for calving, an urge that males do not have. Males therefore could follow females (or their tracks) or make their own decisions about which routes to take. Consequently, social interactions among caribou could be involved and could drive the formation of spring migration corridors (Dalziel et al. 2016; Webber and Vander Wal 2018). Individual decisions made by some individuals in the herd could drive the formation of migration corridors, with other caribou following a leader (Noyce and Garshelis 2014). Although we had approximately 40 caribou collared each year, which is a sample size regularly observed in other large mammal movement studies, it represented ca. 0.01% of the Rivière-aux-Feuilles caribou herd, which limited our ability to evaluate the effect of social interactions on spring migration behavior. More research would be required to determine how individual caribou use this information across years (e.g., using spatial memory) and whether it is shared with other individuals (e.g., through social interactions).

We showed that habitat types, topography, and weather influenced spring migration trajectories in the relatively pristine environment of northern Quebec. Better understanding where and when animals move between their winter and summer ranges in a mostly pristine environment is key to inform decisions by managers. For instance, our results could be used to model future migration trajectories and speed of caribou under different climate change scenarios. Our observation that caribou migrations were not spatially constrained in their relatively pristine habitat differed entirely from studies on other migratory mammals occurring in more disturbed environments, where studies have shown that animals often were confined to narrow corridors with migratory bottlenecks (Sawyer et al. 2005; Seidler et al. 2015). Given the spatial variation in migration corridors used by caribou over the years (Fig. 5), and the potential benefits for caribou to dynamically change their migration corridors, we recommend limiting human disturbances over vast areas between winter and summer ranges of caribou. This could be particularly challenging as this area is slated to be developed in the future (Berteaux 2013).

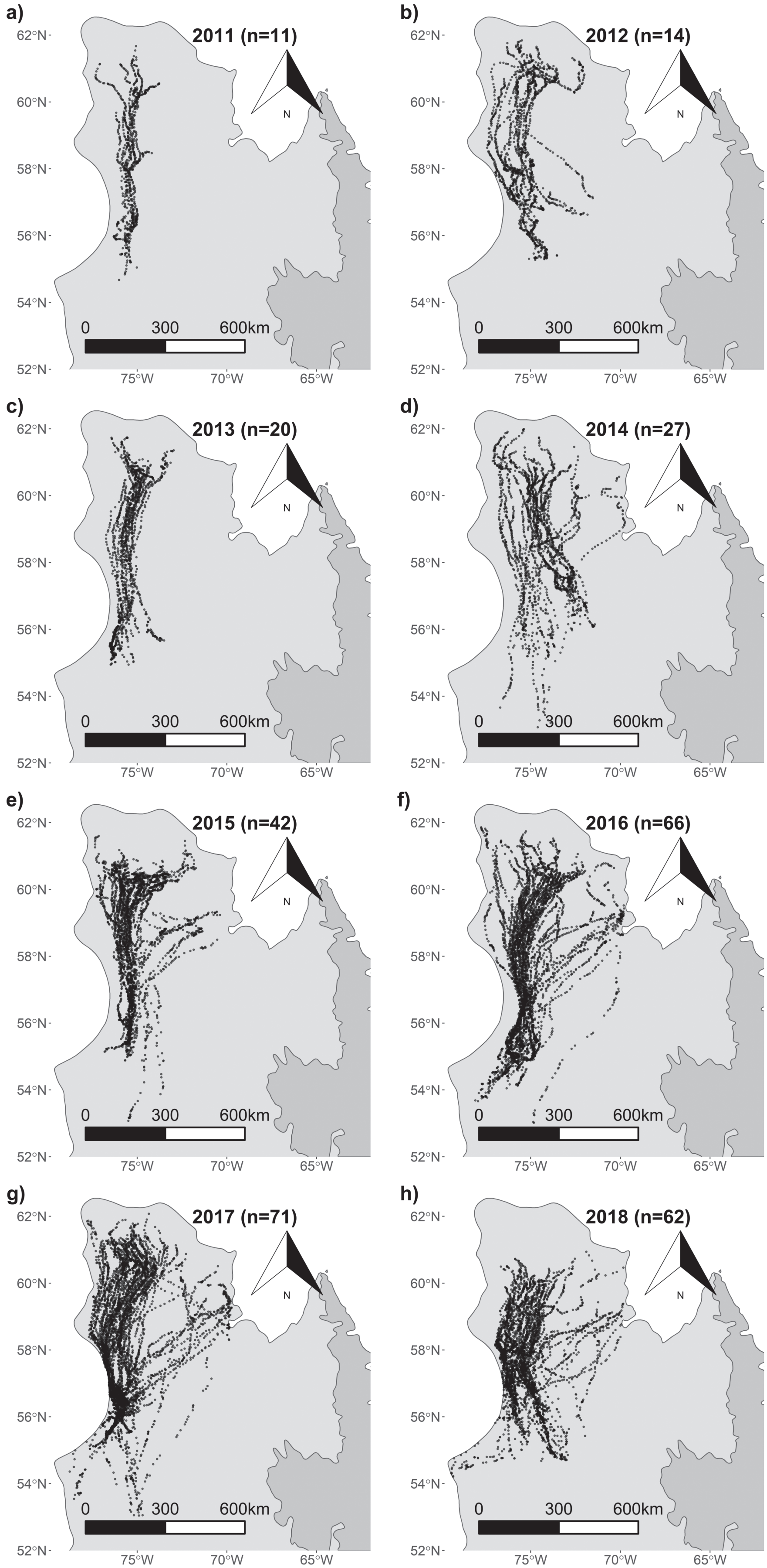

Fig. 5.—Spatial variation of spring migration trajectories of migratory caribou in northern Québec, Canada. Some years, caribou used well-defined corridors (e.g., 2013), whereas other years their corridors were diffuse or absent (e.g., 2014).

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Sensitivity analyses of the number of random paths.

Supplementary Data SD2.—Spatial predictions using the best-supported model.

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