1	Running header:	Caribou	migration	trajectory	and speed
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3	Determinants of migration trajectory and movement rate in a long-distance
4	terrestrial mammal
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19 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, 20 but evaluating the determinants of migration trajectory and movement rate in declining populations 21 facing relatively low levels of human disturbance can provide new and valuable insights on the 22 behavior of wildlife in natural environments. Here, we used an adapted version of path selection 23 functions and quantified the effects of habitat type, topography, and weather, on 313 spring migrations 24 by migratory caribou (*Rangifer tarandus*) in northern Ouébec, Canada, from 2011 to 2018. Our results 25 showed that during spring migration, caribou selected tundra and avoided water bodies, forest, and 26 27 higher elevation. Higher precipitation and deeper snow were linked to lower movement rates. Weather 28 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 29 30 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, 31 32 but we also observed that caribou migrations were not spatially constrained. Better knowledge on 33 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 34 of caribou under different climate change scenarios. 35

36

37 Keywords

38 Declining population, Eastern migratory caribou, movement, Nunavik, *Rangifer tarandus*, resource
 39 selection, Rivière-aux-Feuilles caribou herd

Migration is a behavior observed in many animal taxa, from small insects to large baleen whales 41 (Dingle and Drake 2007; Sinclair et al. 2011). Animals can migrate over different time scales varying 42 from daily (e.g., zooplankton) to seasonal migrations (e.g., wildebeest Connochaetes taurinus), and can 43 cover distances of up to thousands of kilometers, such as in the Arctic tern (*Sterna paradisaea*; 44 Egevang et al. 2010) or humpback whale (*Megaptera novaeangliae*; Stevick et al. 2010). Although 45 migrations can induce high energetic costs that potentially can reduce fitness (Lok et al. 2015), animal 46 47 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 48 49 benefits such as reduction in predation risk and increased access to mates and high-quality forage 50 (Fryxell and Sinclair 1988; McKinnon et al. 2010; Bischof et al. 2012; Middleton et al. 2018). There is, 51 however, increasing evidence that human activities can influence the cost-benefit trade-offs of animal 52 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 53 54 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 55 demographic, ecological, and evolutionary impacts (Holdo et al. 2011; Bauer and Hoye 2014; Seidler 56 et al. 2015; Turbek et al. 2018). We have, however, a poorer understanding of how climate related 57 factors may affect terrestrial migratory populations. Studying migratory patterns of animals living in 58 pristine environments could provide valuable insights about their natural behaviors. 59

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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, and 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 66 caribou often travel > 40 km per day (Le Corre et al. 2017). Calving is believed to be synchronized 67 with the annual peak in resource availability on calving grounds, and trophic mismatches caused by 68 climate change have been observed elsewhere (Post and Forchhammer 2008), but not in northern 69 Québec (Le Corre et al. 2017). Fall migrations generally are much more diffuse than spring migrations 70 and include long pauses ("stopovers") during the rut or to forage (Le Corre et al. 2017). Although 71 72 human disturbances are present on caribou wintering grounds, they are much scarcer during caribou 73 spring migration and on the summer grounds (Plante et al. 2018).

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75 A better understanding of the factors influencing caribou migration patterns in a region where human 76 footprint is low would provide valuable insights to inform management decisions and recovery of this 77 species. For instance, studying migratory trajectories in natural environments could inform about the 78 potential impacts of climate change, and help identify critical areas for natural connectivity. Here, we 79 tested the effect of habitat type, topography, and weather, on the trajectory and movement rate of 80 caribou during spring migrations, using an adapted form of path selection functions. We hypothesized that caribou would minimize energetic costs of travelling during spring migration. Based on previous 81 82 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 83 (Table 1). We also predicted that caribou would reduce their movement rate when faced with harsher 84 environmental conditions such as higher precipitation and deeper snow (Table 1). 85

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MATERIALS AND METHODS

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Study area.—The study area encompassed ca. 300,000 km² in northern Québec, Canada (Figure
1). The caribou population under study, the Rivière-aux-Feuilles migratory caribou population, has

91 undergone a 68% decline, from ca. 628,000 to 199,000 individuals, between 2001 and 2016 (Couturier et al. 2004; MFFP unpubl. data). The winter range of the Rivière-aux-Feuilles migratory caribou herd is 92 located in the southern portion of their annual distribution and is dominated by black spruce (Picea 93 mariana) stands with tamarack (Larix laricina), interspersed with low vegetation composed of shrubs 94 and lichens (Latifovic and Pouliot 2005). The calving and summer ranges are located in the northern 95 part of their annual distribution and mainly are covered by arctic tundra dominated by shrubs (Salix sp. 96 97 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 98 99 precipitations were 1077 mm, most of which felt as snow between October and March (Berteaux et al. 100 2018).

101 Animal capture.—Between 2011 and 2018, we captured male and female migratory caribou 102 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 hours. 103 104 We avoided collaring individuals moving together by spreading captures over several thousands km². 105 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, 106 handling, and monitoring of caribou followed ASM guidelines and were approved by the Canadian 107 Council on Animal Care and the Animal Care Committees of Université Laval and MFFP (permit # 108 2011039). 109

110 *GPS data processing.*—We removed 5 locations with dilution of precision (DOP) > 10 to 111 increase spatial accuracy and manually investigated all animal movements faster than 5 km/h, which 112 led us to remove 7 additional locations (< 0.02% of the dataset) that showed unusual movement 113 trajectory and speed. Our cleaned GPS dataset (n = 26,712 locations) had an average fix success rate of 114 97%. We assessed departure and arrival dates of spring migrations by looking at abrupt changes in 115 caribou movement patterns. We characterized movements of caribou using First-Passage Time (Fauchald and Tveraa 2003), which summarizes the velocity and tortuosity of movement 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 123 124 movement rate by caribou, we conducted path selection functions (Zeller et al. 2012; Carvalho et al. 125 2016). Path SF compare environmental attributes along an animal's utilized path to environmental 126 attributes that could have been encountered along other available paths (Cushman and Lewis 2010; 127 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 128 reordering each step (i.e., a step is the vector connecting 2 consecutive GPS locations) composing the 129 130 real observed path (Figure 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 131 the animal could have taken between the same migration endpoints. Caribou paths were composed of 132 90 ± 22 (mean $\pm SD$) steps and we characterized the real and random paths by extracting elevation, 133 habitat types, and weather variables, at each inflexion point (each step). We extracted elevation from a 134 digital elevation model with a 100 m resolution. We extracted habitat types from a vegetation map 135 (Végétation du Nord Québécois 2018) provided by the MFFP. Minimum mapping unit size was 16 ha 136 for polygons with vegetation and 3 ha for wetlands and water bodies. We divided habitat types into 137 138 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 139 snow; kg/m^2), snow depth (m), snow cover (%), and snowmelt (kg/m^2). We extracted all weather 140

141 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.

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).

151 To carry out the Path SF analysis, we ran conditional logistic regression models to compare real 152 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 153 154 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 155 paths. Because inference from use-available design in habitat selection studies can be influenced by the 156 availability sample (Northrup et al. 2013), we ran sensitivity analyses. Based on the results of 157 sensitivity analyses, we undertook the final analyses with a ratio of 1 used path compared to 100 158 random paths simultaneously, which was well above the threshold where the coefficients for all 159 160 covariates started to stabilize (Supplementary Data S1).

161

For the Path SF 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.

166	We included interactions with movement rate to determine if elevation, weather, and habitat type,
167	influenced the probability of observing a high- or low-speed movement trajectory. We ran conditional
168	logistic regressions for each sex separately and we validated the best supported models using k-fold
169	cross validation following Johnson et al. (2006). Multicollinearity was low with all VIF < 1.5 (Graham
170	2003). We carried out all data processing and statistical analyses in R 3.6.2 (R Core Team 2019).
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173	RESULTS
174	Between 2011 and 2018, we monitored 48 male and 143 female migratory caribou and analysed 313
175	spring migrations (males = 65, females = 248). Likelihood ratio tests revealed no significant
176	differences between male and female spring migration duration (mean = 48.3 days, $\chi^2 = 0.22$, $P = 0.6$)
177	or migration length (mean = 587 km, $\chi^2 = 0.23$, $P = 0.6$). Departure ($\chi^2 = 18.3$, $P < 0.001$) and arrival
178	$(\chi^2 = 22.3, P < 0.001)$ dates of spring migrations were earlier for females than males. Average female
179	spring migration departure and arrival were on Julian dates 111.8 (22 April) and 161.3 (10 June),
180	respectively, while average spring migration departure and arrival were respectively 5.7 and 6.6 days
181	later for males.

182

183 The best supported Path SF model for both females and males was the complete model (Table 2).

184 According to the Δ BIC values of each model (Table 2) and β coefficients (Table 3), we observed that

185 female path selection was influenced by (in decreasing order of importance) habitat types, weather, and

186 elevation, whereas male path selection was influenced by habitat types, elevation, and weather.

187 Movement rate was included in the best supported models for both sexes, but our results suggest that

188 the interaction between movement rate and the other covariates had stronger support for females (Table

189 2, model 8, \triangle BIC = 729; Table 3) than for males (Table 2, model 8, \triangle BIC = 47; Table 3).

191 Compared to associated random trajectories, female caribou selected lower elevation, with higher snow cover, lighter snowmelt, and thinner snow depth (Table 3, Figure 3). The relative probability of 192 selection of high-speed steps by female caribou was higher at lower air temperature and lower 193 precipitation (Figure 3). Finally, female caribou selected tundra and erect shrub tundra more strongly 194 than shrub tundra (i.e., the reference category) and females avoided forests and water bodies (Table 3), 195 but the relative probability of selection of (frozen) water bodies increased with increasing movement 196 rate of the animal (Figure 3). Male selection of spring migration trajectories was similar to females but 197 was not influenced by snowmelt. The interactions between movement rate and weather variables also 198 199 had less support (Table 3). The selection of high-speed steps by male caribou was more likely on water 200 bodies and at lower precipitation (Figure 4). The best supported models for both sexes were robust, with K-fold cross validation of 0.97 ± 0.01 (mean \pm sd) and 0.91 ± 0.04 for females and males, 201 202 respectively.

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DISCUSSION

205 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 206 207 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, 208 namely deeper snow depth and higher precipitations, were linked to slower migrations, as predicted. 209 We also showed that weather had a stronger effect on female migration trajectory and speed than for 210 males. Finally, our results showed that the duration (ca. 48 days) and length (mean of 587 km) of the 211 caribou spring migration were similar for males and females, but that females started (22 April) and 212 ended (10 June) their spring migration about 6 days earlier than males. 213

215 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 216 are well adapted to snowy environments and during spring migration both males and females selected 217 areas with more snow cover. We found, however, that caribou avoided deep snow during migration, 218 probably due to the higher energetic costs of travelling in deeper snow (Fancy and White 1987). We 219 also showed that environmental conditions seemed to affect females more strongly than males. We 220 hypothesize that female caribou may need to adjust their migration timing more precisely than males to 221 match environmental cues. Indeed, while both males and females have a protein-deficient diet during 222 223 winter, female energetic demands are higher than for males during the last stage of gestation, which 224 coincides with spring migration (Chan-McLeod et al. 1994; Parker et al. 2005; Barboza and Parker 225 2008). Snow-covered environments during spring migrations prevent caribou from accessing fresh and 226 newly-grown vegetation. Females therefore might seek to adjust their spring migration speed and 227 arrival on calving grounds with vegetation green-up (Post and Forchhammer 2008). We argue that 228 snowmelt is a key environmental cue that occurs before green-up and we showed that the relative 229 probability of selection of high-speed trajectory by females was higher with increasing snowmelt (Figure 3f). We hypothesize that females increase movement rates when snow is melting to reach 230 231 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 232 to reach better snow conditions and avoid walking in melting snow (Laforge et al. 2021), which is 233 energetically costlier (Shepard et al. 2013). Our results also showed that high-speed trajectory was 234 unlikely when precipitation (mainly snow) was higher (Figure 3b). Many studies have investigated the 235 effects of precipitation on migration phenology in mammals and birds (Pettit and O'Keefe 2017; Haest 236 237 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 238

individual's ability to navigate effectively and increase energetic costs of travelling (Fancy and White
1987; Shepard et al. 2013).

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Habitat types and elevation were not used randomly by caribou during their migration. For instance, 242 forested areas were avoided by caribou, similarly to another caribou population in northwestern Alaska 243 (Fullman et al. 2017), potentially to facilitate travel and increase visibility to detect predators from 244 245 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 246 247 bodies were avoided, the relative probability of selection of high-speed trajectory was higher when 248 caribou were found on a water body compared to tundra or erect shrub tundra. Ultimately, we observed 249 that the relative probability of selection of high-speed trajectory was at its highest when caribou were 250 on a frozen water body (positive slope reaching y = 1 in Figures 3a and 4a). The use of frozen water bodies therefore was a major determinant of caribou spring migration movement rates. Knowing that 251 252 caribou rarely swam across water bodies and prefer to circumvent open water (Leblond et al. 2016), we 253 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 254 255 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) 256 and in moose (Leblond et al. 2010), potentially due to the higher energetic costs of travelling (White 257 and Yousef 1978). 258

259

Mapping the predictions from our best model (Supplementary Data S2) 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 (Fig. 5a, c). In other years, 264 however, migration corridors were diffuse or even absent (Fig. 5d). Moreover, the location of spring 265 migration corridors varied annually (Fig. 5). Caribou could use different migration corridors over time 266 to access new resources or to adjust to the weather conditions they encounter during travel. Vegetation 267 grows slowly in the Arctic, and past foraging as well as trampling by caribou could force them to 268 displace their migration corridors to access better-quality or more abundant forage (Ferguson et al. 269 2001; Joly et al. 2010). We also hypothesize that caribou could use different migration corridors over 270 time to reduce their predictability and potentially reduce predation risk. Indeed, searching for prey over 271 272 vast landscapes such as northern Québec might be more costly for predators.

273

We found that females left the wintering grounds and arrived on calving grounds earlier than males. 274 275 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) 276 277 or make their own decisions about which routes to take. Consequently, social interactions among 278 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 279 280 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 281 observed in other large mammal movement studies, it represented ca. 0.01% of the Rivière-aux-282 Feuilles caribou herd, which limited our ability to evaluate the effect of social interactions on spring 283 migration behavior. More research would be required to determine how individual caribou use this 284 information across years (e.g., using spatial memory) and whether it is shared with other individuals 285 286 (e.g., through social interactions).

We showed that habitat types, topography, and weather, influenced spring migration trajectories in the 288 relatively pristine environment of northern Quebec. Better understanding where and when animals 289 move between their winter and summer ranges in a mostly pristine environment is key to inform 290 decisions by managers. For instance, our results could be used to model future migration trajectories 291 and speed of caribou under different climate change scenarios. Our observation that caribou migrations 292 were not spatially constrained in their relatively pristine habitat differed entirely from studies on other 293 294 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. 295 296 2015). Given the spatial variation in migration corridors used by caribou over the years (Fig. 5), and the 297 potential benefits for caribou to dynamically change their migration corridors, we recommend limiting 298 human disturbances over vast areas between winter and summer ranges of caribou. This could be 299 particularly challenging as this area is slated to be developed in the future (Berteaux 2013).

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318	Supplementary Data
319	Supplementary Data S1.— Sensitivity analyses of the number of random paths.
320	Supplementary Data S2.— Spatial predictions using the best supported model.
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469

471 Figure legends

Fig 1.—GPS locations (n = 26,712) of male (n = 48) and female (n = 143) caribou used to assess path 472 selection during spring migrations (n = 313) in 2011 – 2018 in northern Québec, Canada. 473 Fig. 2.—Design of the path selection function. We determined the available path (grey dotted line) by 474 randomly reordering the vectors (each step between 2 consecutive locations) that composed a real 475 migration path (black solid line). This approach allowed us to compare random migration paths that 476 started from and ended in the same locations as the true migration paths. We characterized the path by 477 extracting environmental variables at each inflexion point (black and grey dots). This illustration 478 479 represents a simplified path; observed caribou paths were composed of 90 ± 22 (mean \pm sd) steps on 480 average. Fig. 3.—Results of the best supported conditional logistic regression model describing spring migration 481 482 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 483 85th percentiles observed in the dataset, respectively. 484 485 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 486 for weather variables were obtained in erect shrub tundra. Low and high values correspond to the 15th 487 and 85th percentiles observed in the dataset, respectively. 488 Fig. 5.—Spatial variation of spring migration trajectories of migratory caribou in northern Québec, 489 Canada. Some years, caribou used well-defined corridors (e.g. 2013), whereas other years their 490 corridors were diffuse or absent (e.g. 2014). The vertical red line serves as a fixed spatial reference to 491 compare among years. 492

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	Miller and Gunn 1986,
	to cross and increase risks of drowning.	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	Fancy and White 1987
	sinking depth.	

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

Model	Covariates included	Male		F	Female		
		LL	Δ BIC	Wi	LL	Δ BIC	Wi
1	None	-43693	2095	0	-198928	8472	0
2	Elevation	-43500	1723	0	-198906	8443	0
3	Temperature + Precipitation + Snow depth + Snow cover + Snowmelt	-43590	1955	0	-198507	7703	0
4 ^a	Erect shrub tundra + Heathlands + Forest + Water + Tundra + Other	-43001	790	0	-195689	2083	0
5	Model 2 + Model 3	-43389	1568	0	-198491	7687	0
6	Model 2 + Model 4	-42805	413	0	-195616	1951	0
7	Model 3 + Model 4	-42808	470	0	-195072	920	0
8	Model 2 + Model 3 + Model 4	-42590	47	0	-194969	729	0
9	Speed \times Model 2	-43465	1680	0	-198900	8460	0
10	Speed \times Model 3	-43557	1968	0	-198303	7383	0
11	Speed \times Model 4	-42964	808	0	-195451	1708	0
12	Speed \times Model 5	-43321	1523	0	-198278	7361	0
13	Speed \times Model 6	-42738	383	0	-195368	1572	0
14	Speed \times Model 7	-42732	476	0	-194623	198	0
15	Speed \times Model 8	-42481	0	1	-194509	0	1

^a Reference category = shrub tundra

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

	Male			Female		
Covariates	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 \times Elevation	0.003	0.002	0.004	-0.001	-0.001	0.000
Speed \times 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 \times Snow depth	0.104	-1.295	1.504	-0.489	-0.946	-0.033
Speed \times Snow cover	-0.137	-0.481	0.207	-0.199	-0.314	-0.084
Speed \times Snowmelt	0.031	-0.069	0.132	0.206	0.154	0.258
Speed \times Erect shrub tundra	0.041	-0.134	0.216	-0.244	-0.330	-0.158
Speed \times 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 \times 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













Figure 4



Figure 5



Supplementary Data S1

Results of the sensitivity analyses testing the relationship between the number of random paths used to define availability in Path Selection Functions and the resulting selection coefficients. Coefficients stabilized as the number of random paths increased. We ran our final models with 100 random paths to define availability, which is above the threshold over which all coefficients stabilized.



Number of random path

Supplementary Data S2

Spatial prediction of the best supported model describing the relative probability of path selection during spring migration of female caribou on 20 May 2013 in northern Québec, Canada. Spring migrations of caribou did not seem to be spatially constrained by weather, topography, nor habitat types during our study.

