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Running header: Disturbance and weather affect movement

**Effects of human-induced disturbances and weather on herbivore movement**

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21 Human-caused habitat disturbances and climate change are leading threats to biodiversity. Studying the  
22 impacts of human activities on wildlife from a behavioral perspective is a relevant starting point to  
23 understand the mechanisms underlying population and species resistance and resilience to disturbances.  
24 In this study, we assessed the effects of weather (temperature and precipitation), habitat disturbances  
25 (roads and clearcuts), and natural habitat types on the space use patterns of a threatened boreal  
26 population of woodland caribou (*Rangifer tarandus caribou*). An extensive dataset of 288,665  
27 relocations from 50 adult females outfitted with GPS collars over 7 years in the boreal forest of  
28 Québec, Canada was used to evaluate residency time in natural and disturbed habitats for five distinct  
29 biologically defined periods. The most parsimonious linear mixed-effects model for each period  
30 showed that individuals stayed longer in more natural habitat types. During calving and summer,  
31 residency time decreased with increasing road density, whereas residency time decreased with  
32 increasing temperature during winter and spring. We found no evidence of a synergistic effect between  
33 daily weather and human disturbances on movement behavior of caribou, but consider their respective  
34 influence as additive. We also showed large individual variation in residency time, except during the  
35 calving period. Lower individual variation in residency time during calving may be explained by strong  
36 evolutionary constraints on behavior faced by females to ensure protection and survival of their  
37 offspring. Based on our results, we suggest keeping large patches of suitable and roadless habitat for  
38 caribou to favor the spacing-out antipredator strategy exhibited by females during calving. By tracking  
39 individuals over several complete annual cycles, we showed variation in the effects of daily weather  
40 and human disturbances on residency time across biological periods. Our study highlights that the  
41 inclusion of daily weather variables helps better understand space-use patterns of a threatened species.  
42  
43 Key words: boreal forest, climate, first-passage time, GPS-tracking, habitat use, *Rangifer tarandus*  
44 *caribou*, residency time, ungulate

45

46 Earth has now entered its 6<sup>th</sup> mass extinction of species and human activities are at the center of this  
47 biodiversity crisis (Ceballos et al. 2015; Sánchez-Bayo and Wyckhuys 2019). Human-induced habitat  
48 loss and climate change modify environmental conditions and influence the abundance and distribution  
49 of species as well as the structure of communities (Schmiegelow and Mönkkönen 2002; Fahrig 2003;  
50 Williams and Jackson 2007). The way disturbances affect species–habitat relationships (Bachand et al.  
51 2014), population dynamics (Laliberté and Ripple 2004), community structure (Williams et al. 2008;  
52 Velásquez-Tibatá et al. 2013), and intraspecific and interspecific interactions (Muhly et al. 2011;  
53 Steyaert et al. 2016) is of critical importance. Quantifying the effects of human disturbances on wildlife  
54 will allow predicting more efficiently the consequences of future environmental conditions on  
55 biodiversity.

56 Wildlife–habitat relationships can be studied by looking at behavioral traits, such as space use  
57 and movement of individuals on the landscape. For instance, recent studies suggest that human  
58 disturbances, such as roads, generally reduce movement and may even disrupt animal migrations  
59 (Seidler et al. 2015; Bauduin et al. 2018; Tucker et al. 2018). Considering that movements within and  
60 among seasonal ranges follow a strategy to minimize costs while maximizing access to high-quality  
61 resources (i.e., optimal foraging strategy; MacArthur and Pianka 1966; Schoener 1971; Pyke 1984),  
62 limits on such movements can ultimately affect reproduction and population growth (Fryxell and  
63 Sinclair 1988; Middleton et al. 2018). Indeed, many studies have shown that behavioral responses to  
64 disturbances can influence individual performance (survival: McLoughlin et al. 2005; reproductive  
65 success: Dussault et al. 2012; Leclerc et al. 2014) and ultimately even macro-evolutionary patterns  
66 (speciation and adaptive radiation: Storch and Frynta 1999; Remes 2000; Morris 2003). Consequently,  
67 studying the impacts of disturbances from a behavioral perspective is a relevant starting point to

68 characterize, understand, and integrate the mechanisms underlying population and species resilience to  
69 disturbance.

70 One can assume that the mobility of an individual will partly define its capacity to adjust its  
71 movements to changing environmental conditions. For example, Schloss et al. (2012) showed that the  
72 limited movement capacity of primates will limit their ability to keep pace with climate change, while  
73 the more mobile artiodactyls are expected to be able to track future shifts in suitable climates more  
74 easily. Also, anthropogenic disturbances, such as roads or fences, can hinder a species' mobility and  
75 potentially their ability to cope with the effects of climate change (Seidler et al. 2015; Tucker et al.  
76 2018). On the other hand, female mule deer (*Odocoileus hemionus*) showed higher rates of travel in  
77 areas with high natural-gas development, which resulted in early arrival in their summer range  
78 (Lendrum et al. 2013). By studying the effects of anthropogenic disturbances and weather  
79 simultaneously, we could better understand if weather and anthropogenic disturbances shape animal  
80 movement additively or synergistically. A synergistic effect between weather and anthropogenic  
81 disturbances could exacerbate negative impacts of human disturbances on wildlife with future climate  
82 change, or may compensate some of the negative impacts of human disturbances depending on the  
83 direction of interactions between weather and disturbance-related factors

84 Boreal forests provide excellent study systems for investigating the effects of meteorological  
85 conditions and anthropogenic disturbances on wildlife–habitat dynamics because weather is expected  
86 to vary more at higher latitudes in response to climate change (IPCC 2007). Boreal species have  
87 evolved adaptive strategies to accommodate long-term variation in the intensity and frequency of  
88 natural disturbances such as wildfires, windthrows, and insect outbreaks (Östlund et al. 1997; McRae et  
89 al. 2001). Across the southern extent of the boreal forest, however, the rate of anthropogenic activity  
90 and resulting forest change now outpace that of natural disturbances as well as the resilience of affected  
91 communities (Vitousek et al. 1997; Sanderson et al. 2002; Cyr et al. 2009). Herbivore species can be

92 particularly sensitive to habitat disturbances that may modify food availability and quality, as well as  
93 shelter (Stien et al. 2010; Leclerc et al. 2012a). Studying boreal herbivores can thus provide us with  
94 unique opportunities to investigate the mechanisms through which disturbances and weather affect  
95 ecological communities.

96 The caribou (or reindeer in Eurasia; *Rangifer tarandus*) is a well-studied and highly mobile  
97 species inhabiting boreal and arctic ecosystems, and many populations are declining across its  
98 circumpolar range (Vors and Boyce 2009; Hebblewhite 2017). In Canada, the boreal population of  
99 woodland caribou (*Rangifer tarandus caribou*; hereafter referred to as caribou) is considered an  
100 irreplaceable component of biodiversity (COSEWIC 2011) and is considered threatened according to  
101 the Species at Risk Act (SARA 2002). Caribou also have strong socioeconomic and cultural value,  
102 being an important consideration during forest certification and a subsistence species for Aboriginal  
103 peoples (Dzus et al. 2010).

104 Here, our main goal was to assess the additive and potentially synergistic effects of weather  
105 (temperature and precipitation) and habitat disturbances (roads and clearcuts) on the space-use patterns  
106 of caribou. To that end, we used a unique, detailed dataset of GPS relocations of boreal caribou  
107 spanning 7 years. More precisely, our objectives were to determine 1) if the time spent by a caribou in  
108 a given area (i.e., residency time) depends on daily weather and habitat disturbances, and 2) test if daily  
109 weather effects on residency time vary depending on whether the animal occupies a disturbed habitat or  
110 not. Knowing that caribou avoid habitat disturbances (Leclerc et al. 2012b, 2014) and given that  
111 ungulates modify their behavior in response to weather to reduce thermoregulatory costs (Dussault et  
112 al. 2004), we predicted that 1) residency time will increase with a decreasing proportion of disturbed  
113 habitats and harsher daily weather (more precipitation and extreme temperatures), 2) daily weather will  
114 have less effect than habitat disturbances on residency times, and 3) the effect of disturbed habitats on  
115 residency time will be modulated by daily weather; residency time in disturbed landscape will be

116 shorter with harsher daily weather owing to the poor cover from harsh conditions provided by disturbed  
117 landscapes.

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119

## MATERIAL AND METHODS

120 *Study area.*— Our study area was located north of Lac Saint-Jean and the Saguenay River in  
121 Québec, Canada, and covers approximately 31,000 km<sup>2</sup> (Fig. 1), centered on Pirabe Lake in the north  
122 (49°42'– 51°00'N, 71°10'– 72°09'W) and Portneuf Lake in the south (48°21'– 49°45'N, 69°51'–  
123 71°12'W). The vegetation in the southern part of the study area was dominated by black spruce (*Picea*  
124 *mariana*) with balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), white spruce (*Picea*  
125 *glauca*), trembling aspen (*Populus tremuloides*) and jackpine (*Pinus banksiana*). The northern region  
126 of the study area was dominated by old-growth coniferous forest and open forest with black spruce,  
127 balsam fir and jackpine stands. Mean annual temperatures range between -2.5 and 0.0 °C (extremes  
128 ranging from -38 to 33 °C) and mean annual precipitation between 1,000 and 1,300 mm, of which 30-  
129 35% falls as snow (Robitaille and Saucier 1998). Moose (*Alces americanus*), gray wolves (*Canis*  
130 *lupus*), and black bears (*Ursus americanus*) are the other large mammal species found in the study area.  
131 Industrial forestry is the main source of disturbance, with a logging history of ~50 years for the  
132 southern and ~25 years for the northern parts of the study area, resulting in ~59% and ~39% of their  
133 surface being under the influence of past fires, clearcuts, and forest roads when data were collected  
134 (Environment Canada 2012).

135

136 *Caribou capture and telemetry survey.*— We captured, radiocollared, and monitored 50 adult  
137 (>1.5 year of age at the time of capture) female caribou from 2004 to 2010 (13 to 24 per year for a total  
138 of 125 caribou-years, yielding 293,841 relocations) using global positioning system (GPS) collars  
139 (Lotek models 2 200L and 3 300L, and Telonics TGW-4680). Individuals were captured by net-

140 gunning from a helicopter and recaptured periodically to retrieve data, change battery packs, or remove  
141 collars. Collars were also recovered following failure or death of an individual. Collars were  
142 programmed to acquire and record a GPS relocation at slightly different intervals (1-4 h). In addition,  
143 owing to occasional failure in position acquisition, the actual sampling interval also was not as regular  
144 as programmed, causing the mean sampling interval in our dataset to be  $2.3 \pm 1.7$  h (*SD*). Some  
145 individuals were tracked over several non-consecutive periods, which were thus considered as distinct  
146 movement bouts in the subsequent analyses (see below for details), referred to as “tracks” ( $n = 70$   
147 tracks in total; Supplementary Data SD1). The cumulated time during which individual females were  
148 tracked ranged from ca. 6 weeks to ca. 5 years (see Supplementary Data SD1).

149 We surveyed only females, which due to their strong association with calves constitute the most  
150 vulnerable portion of the population (Leclerc et al. 2014) and are thus strongly linked to population  
151 dynamics (Barten et al. 2001). Caribou behavior changes throughout the annual cycle, so we conducted  
152 our analyses for five relevant biological periods as defined previously in our study area (Hins et al.  
153 2009): spring (15 April – 14 May), calving (15 May – 14 June), summer (15 June – 14 September), rut  
154 (15 September – 14 November) and winter (15 November – 14 April).

155 Our study followed American Society of Mammalogists guidelines (Sikes et al. 2016) and was  
156 carried out in strict accordance with the recommendations of the Canadian Council on Animal Care.  
157 Both captures and manipulations of study animals were approved by the Animal Welfare Committee of  
158 the Université du Québec à Rimouski (certificate #36-08-67). Captures were conducted on public  
159 lands, under the supervision of the Québec Government (i.e., Ministère des Forêts, de la Faune et des  
160 Parcs, hereafter MFFP), hence no specific permissions were required.

161

162 *Habitat variables.*— We used 1:20,000 digitized ecoforest maps published in 2000 by the MFFP  
163 to determine land-cover classes, and we updated these maps annually to include new habitat

164 modifications resulting from forestry practices and natural disturbances. Minimum mapping unit size  
165 was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies). Based on studies  
166 conducted in the same system (Hins et al. 2009; Leclerc et al. 2012b, 2014; Beauchesne et al. 2013,  
167 2014; Leblond et al. 2016a), we defined undisturbed habitat types as mature coniferous stands, while  
168 anthropogenic features consisted of clearcuts of varying age (0-5 and 6-20 years old) and roads. We did  
169 not include regenerating stands (20-40 years old) in our analyses due to multicollinearity. The effects of  
170 time since logging within each age category are considered minimal (Hins et al. 2009). We also  
171 characterized the topography of caribou habitat using elevation and terrain ruggedness. Terrain  
172 ruggedness was measured as the coefficient of variation of elevation (Leclerc et al. 2012b). We  
173 extracted habitat data for each GPS relocation using an 800-m radius buffer, based on results from  
174 preliminary first-passage time analyses on the entire study population (see below).

175

176 *Daily weather data.*— Daily weather data were produced by Natural Resources Canada and  
177 interpolated at a spatial resolution of 10 km. Daily gridded values of temperature and total precipitation  
178 were extracted for the years 2004-2010 for our study region, based on the methodology described in  
179 Hutchinson et al. (2009) and Hopkinson et al. (2011). We extracted mean daily temperature and  
180 precipitation values at each GPS relocation.

181

182 *Residency time assessed using first-passage time.*— We used a two-step approach based on first  
183 passage time (FPT) analysis (see Fauchald and Tveraa 2003 for more details, especially their Figure 3)  
184 to estimate the time spent by an individual in an area (i.e. residency time). FPT is a measure of the time  
185 used by an individual to cross a circle of given radius (i.e. different radii referring to different scales)  
186 centered on each GPS relocation, and is thus related to residency time along each individual path. In a  
187 first exploratory step, we aimed at obtaining a general picture of the spatial scales at which individuals



188 of our study population were using their habitat. We recalculated the positions along the tracks at 100-  
189 m intervals using the method provided by (“rediscretizing”; Calenge 2006) and then calculated the  
190 variance of the natural log in FPT [ $var(\log(\text{FPT}))$ ], following Fauchald and Tveraa (2003). FPT was  
191 calculated over a sequence of spatial scales with radii ranging from 100 to 15,000 m, using 100-m  
192 increasing intervals. Only tracks that covered more than 6 months of consecutive tracking ( $n = 51$  out  
193 of the 70 tracks) were used in this first step to avoid using tracks that would represent only a very short  
194 period of the annual cycle. The results were then averaged to investigate the occurrence of peaks in  
195  $var(\log(\text{FPT}))$ , indicative of spatial scales at which area-restricted search behavior takes place. We  
196 observed a peak in variance at 800 m (Fig. 2) and this spatial scale was used in subsequent analysis.

197 In a second step, we calculated residency (in days) time using FPT at each actual GPS relocation  
198 within a circle of radius (scale) of 800 m using the complete set of tracks ( $n = 70$ , see Supplementary  
199 Data SD1). Considering that successive GPS relocations could be spaced by a few or several meters,  
200 the time needed to cross a 800-m radius circle centered on each GPS relocation (i.e. residency time)  
201 could thus be long if relocations are close along a path or short if relocations are spaced by several  
202 meters (meaning in this case that distance covered in the fixed time interval between successive  
203 relocations is large). Habitat and weather covariates were extracted over circular areas with a radius of  
204 800 m centered on each relocation. Relocations for which environmental or habitat data were not  
205 available were removed from the datasets. In addition, FPT cannot be estimated at the beginning and  
206 end of any given track for a number of relocations. This resulted in a final sample size of 288,665 GPS  
207 relocations, with an average of 5,773 relocations per individual.

208 We processed all movement data using R 3.2.3 (R Development Core Team 2017). We used the  
209 *adehabitatLT* package v.0.3.16 (Calenge 2006) for FPT calculations. We extracted environmental data  
210 using the Geospatial Modelling Environment v.0.2.7.0 (Beyer 2012), which uses ArcGIS v.10.0 (ESRI  
211 2011) as the computation engine.

212 *Statistical analyses.*— We used daily average of FPT to reduce pseudo-replication and to  
213 compensate for slightly different sampling rates among individuals. We log-transformed daily average  
214 of FPT to fulfill all statistical assumptions. We modeled variation in  $\log(\text{FPT})$  of caribou using linear  
215 mixed-effects models with the *nlme* package (Pinheiro et al. 2018) in R 3.4.3 (R Development Core  
216 Team 2017). We controlled for repeated measures by adding individual identity (ID) as a random  
217 intercept and we added Year nested within ID to handle individual variation among years. We also  
218 controlled for temporal autocorrelation by adding a first order autocorrelation structure in the model  
219 specifications (Crawley 2007; Pinheiro et al. 2018). Using Akaike’s information criterion (AIC;  
220 Burnham and Anderson 2002), we evaluated, for each biological period separately, a set of 14 plausible  
221 candidate models (Table 1) that combined different additive and interactive effects of continuous  
222 variables describing daily weather (temperature, precipitation), disturbances (proportion of 0-5-years-  
223 old clearcuts, proportion of 6-20-years-old clearcuts, road density), and natural habitat types  
224 (proportion mature coniferous stands, elevation, terrain ruggedness). The candidate models  
225 corresponded to different biological interpretations linked to our hypothesis (Table 1). Given that the  
226 14 candidate models were constructed hierarchically, we did not perform model-averaging and we  
227 selected and discussed only the top-ranked model for each biological period using AIC (Arnold 2010),  
228 although models within  $\Delta\text{AIC} < 2$  were considered competitive. We calculated the relative importance  
229 of each predictor variable with the *MuMIn* package (Barton 2018) and we calculated, for the most  
230 parsimonious model, the proportion of variance explained by fixed and random effects based on  
231 Nakagawa and Schielzeth (2013). We scaled (mean = 0, variance = 1) all predictor variables for easier  
232 model convergence (see Supplementary Data SD2 for raw distribution and the units of variables).  
233 Variance inflation factor for the most parsimonious models were  $< 3$  (Graham 2003) and we examined  
234 the residuals visually to confirm the absence of a clear deviation from normality.

235

236

## RESULTS

237 From the set of 14 candidate models tested, five were retained as competitive for at least one of  
238 the five periods (Table 2). Natural habitat types (coniferous forest, elevation, ruggedness) were retained  
239 in the top-ranked model in all biological periods (Table 2). The top-ranked model also included the  
240 effects of disturbances (clearcuts and roads) during calving, summer, and rut, while daily weather  
241 variables were retained in the top-ranked model during winter, spring, and rut, as well as the most  
242 competitive models during winter and spring. The synergistic effects of human disturbances and daily  
243 weather were not retained in any biological periods in the top-ranked model but was competitive in  
244 winter ( $\Delta AIC = 1.90$ ; Table 2). Total variance, i.e., including fixed and random effects, explained by  
245 the most parsimonious models ranged from 3.2% (calving) to 22.2% (summer; Supplementary Data  
246 SD3).

247 Some general patterns emerged across biological periods. First, daily weather influenced FPT.  
248 We observed a decrease in FPT with increasing temperature during winter, spring, and rut, but we  
249 found no evidence for any effect of precipitation (Tables 3-4). Second, disturbances also influenced  
250 FPT, which decreased with increasing road density and greater proportion of young (0-5-years-old)  
251 clearcuts during calving, summer, and rut (Table 4). Finally, our results showed that variables  
252 considered in the model based on natural habitat types influenced FPT: higher elevation and more  
253 rugged terrain increased FPT in most biological periods, and greater proportion of mature coniferous  
254 stands increased FPT during winter and spring (Tables 3-4, Fig. 3). Effect sizes (Tables 3-4) and the  
255 relative importance (Supplementary Data SD4) of the predictor variables in the models suggest that  
256 natural habitat types were the main factor influencing FPT, while the importance of daily weather and  
257 disturbances on FPT were not consistent across periods. Daily weather was more important during  
258 winter and spring, while disturbances were more important during calving and summer.

259

## DISCUSSION

260

261 Most previous studies on movement and space-use patterns in terrestrial mammals investigated the  
262 effects of disturbed habitat types and linear features such as roads (e.g., Prokopenko et al. 2017;  
263 Monteith et al. 2018). Although some of those studies attempted to control for weather by dividing  
264 annual data into different biological periods (e.g., Leblond et al. 2010; van Beest et al. 2013), the  
265 effects of fine-scale variation in daily weather within a biological period has rarely been investigated  
266 (but see e.g., Monteith et al. 2011; Middleton et al. 2013). Here, we showed that residency time  
267 (assessed using FPT) increased with colder weather and decreasing human disturbances. Those  
268 relationships, however, did not hold in all biological periods. Disturbances had a larger effect on  
269 residency time than daily weather during calving and summer, but this was reversed during winter and  
270 spring. Therefore, our results only partially supported our prediction that daily weather would have a  
271 weaker effect than habitat disturbances on residency time. Our results highlight the importance of  
272 studying animal behavior over complete annual cycles as the effects of weather and disturbances on the  
273 movement may vary seasonally. Finally, we found no evidence that residency time in disturbed habitats  
274 was modulated by daily weather in our study system.

275 Herbivore movement behavior serves several purposes, including finding food resources,  
276 avoiding predators, and finding shelter (Dussault et al. 2004; Leclerc et al. 2012b; Merkle et al. 2016).  
277 Our results suggest that movements of caribou likely aim to reduce predation risk. By increasing  
278 residency time in mature coniferous stands, at higher elevation, and in rugged terrain, caribou can  
279 decrease the rate of encounters with predators such as wolves which usually use lower elevations and  
280 flat terrain (Whittington et al. 2011; Lesmerises et al. 2012). Also, caribou tend to reduce residency  
281 time with increasing road density. The presence of roads is associated with higher encounter rate and  
282 predation risk by wolves (James and Stuart-Smith 2000; Whittington et al. 2011), and roadsides are  
283 highly productive environments that are also selected by other predators of caribou such as black bears,

284 particularly during the onset of bud growth in spring and summer (Bastille-Rousseau et al. 2011).  
285 Avoidance of human disturbances, especially roads, during calving has been shown for boreal caribou  
286 in Québec (Leclerc et al. 2012b). Avoidance of disturbed habitat by females with calves is known to  
287 increase their reproductive success (Leclerc et al. 2014) and likely have impacts at the population level  
288 because calf survival can greatly influence population dynamics (Gaillard et al. 2000). Our results are  
289 in line with previous work on boreal caribou that suggests that the current recession of the southern  
290 limit of this threatened species is linked to anthropogenic disturbances (Schaefer 2003; Vors et al.  
291 2007) via maladaptive behavioral responses (Leclerc et al. 2014; Losier et al. 2015; Lafontaine et al.  
292 2017). Anthropogenic disturbances reduce the area of their prime habitat and trigger the numerical and  
293 functional responses of alternative prey and predators (Seip 1992; Wittmer et al. 2005; Courtois et al.  
294 2008; DeCesare et al. 2010). Reduction of residency time in disturbed landscape and in areas with  
295 higher predation risk was also observed in elk (*Cervus elaphus*). Indeed, elk reduce their rate of  
296 movement and increase their residency time when hunter access (mainly roads) is limited and when the  
297 occurrence of predators is lower (Frair et al. 2005; Cleveland 2012).

298         The strongest negative effect of road density and the strongest positive effects of elevation and  
299 terrain ruggedness were observed during calving and summer: both variables are associated with an  
300 increased avoidance of predation risk. Calving and summer are the most critical periods for female  
301 reproductive success as the calves are highly vulnerable to predation (Pinard et al. 2012; Leclerc et al.  
302 2014). In addition, all females showed similar behavioral responses to natural habitat types and human  
303 disturbances during calving, as shown by the very low variance explained by random effects  
304 (Supplementary SD3). We consider that natural selection may have shaped such behavioral responses  
305 during this critical phase. In contrast, the higher individual variation in movement behavior measured  
306 during other biological periods could indicate that appropriate responses to human disturbances and  
307 adverse weather conditions can be achieved through different tactics that maintain phenotypic

308 variation. However, further studies will be necessary to confirm this hypothesis, and would for instance  
309 involve measurements of indices of individual state (e.g., body mass, stress hormone levels) and fitness  
310 (e.g., calf survival).

311 Individual variation in residency time could be due to differences in individual state, age, or  
312 personality (Réale et al. 2010; Sih et al. 2015). While we controlled for daily weather, some variation  
313 across and within years could be explained by other environmental variables related to daily weather  
314 that were not included in this study, such as snow depth or temporary summer drought (Vandal and  
315 Barrette 1985). Daily weather can influence the phenology of insects' emergence, snow and ice  
316 melting, or rain-on-snow events, which in return could also modulate animal movement (Putkonen and  
317 Roe 2003; Stien et al. 2010; Loe et al. 2016; Leblond et al. 2016b).

318 Caribou are large mammals well adapted to snowy environments (Telfer and Kelsall 1984),  
319 which might explain why we did not find any influence of precipitation on residency time (Table 3-4).  
320 Caribou did respond, however, to temperature. During winter and spring, higher temperature decreased  
321 residency time, which likely increases energy expenditure on movement by caribou during this period  
322 of lower food availability. Higher temperature during winter and spring is expected in boreal and arctic  
323 regions due to climate change and will likely affect caribou movement (IPCC 2007). Climate change is  
324 also expected to increase rain-on-snow events, which are known to limit food access and reduce fitness  
325 of *Rangifer* in arctic ecosystems (Stien et al. 2012). The effect of rain-on-snow events on caribou  
326 inhabiting the boreal forest, however, may be limited because caribou can have access to other food  
327 sources such as arboreal lichen (Rominger et al. 1996; Terry et al. 2000). Increased temperature during  
328 spring will likely speed up the green-up period, which may limit the duration of a rich diet quality  
329 during the last phases of gestation for caribou. Overall, we showed that daily temperature did influence  
330 the behavior of caribou, but the consequences of daily weather on fitness in our study population  
331 remain unknown.

332 By combining daily weather variables and habitat disturbances in the same models, we showed  
333 that their effects on residency time were additive. The absence of synergistic effects between habitat  
334 disturbances and daily weather on residency time in our study may be explained by the low variability  
335 of habitat disturbances at the spatial scale we conducted our analysis. Low variability in habitat  
336 disturbances at an 800-m scale is expected in caribou as they tend to avoid human disturbances at much  
337 larger spatial scales (Leclerc et al. 2012b; Leblond et al. 2013a; Fortin et al. 2013).

338 Using detailed behavioral information from threatened boreal caribou, we evaluated the effect of  
339 daily weather, habitat disturbances, and natural habitat types on residency time. We showed that  
340 including daily weather variables in models can improve our understanding of space use patterns for a  
341 wide-ranging ungulate. Also, during calving and summer, females decreased residency time with  
342 increasing road density, a disturbance type associated with facilitated movement for predators (Dickie  
343 et al. 2017), a higher encounter rate with wolves (Whittington et al. 2011), and a higher predation risk  
344 for adult females (Leblond et al. 2013b) and their calves (Dussault et al. 2012; Leclerc et al. 2014).  
345 Based on our results, we suggest keeping large patches of suitable and roadless habitat for caribou to  
346 favor the spacing-out antipredator strategy exhibited by females during calving. Our study helps  
347 understand how animals react to disturbance across an array of weather conditions and enhances our  
348 capacity to predict how wildlife will be able to adjust to changing future environmental conditions.

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350

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## SUPPLEMENTARY DATA

364

365

366 **Supplementary Data SD1.**— Summary of the GPS tracking of 50 adult female caribou (*Rangifer*  
367 *tarandus caribou*). Some individuals were tracked for several non-consecutive periods (see column  
368 “bout”). The complete database yields a total of 70 bouts with a mean duration of 61.4 weeks (range =  
369 6.3–223.9 weeks).

370

371 **Supplementary Data SD2.**— Distribution of values for each variable in the dataset used to determine  
372 residency time of adult female caribou (*Rangifer tarandus caribou*), based on first-passage time  
373 analyses conducted within 800-m radius circles centered on all successive GPS relocations. Please note  
374 that the distribution shows the raw values, not the scaled values used in the statistical analyses.

375

376 **Supplementary Data SD3.**— Variance explained (%) by fixed and random effects in the most  
377 parsimonious model describing residency time calculated using first-passage time analyses conducted  
378 within 800-m radius circles centered on all successive GPS relocations, for each biological period.

379

380 **Supplementary Data SD4.**— Relative importance of each variable for each biological period in  
381 explaining residency time (assessed using first-passage time analyses conducted within 800-m radius  
382 circles centered on all successive GPS relocations) for caribou (*Rangifer tarandus caribou*) in Canada.  
383 We calculated the relative importance of each predictor variable using the MuMIn package (Barton  
384 2018) in R 3.4.3 (R Development Core Team 2017).

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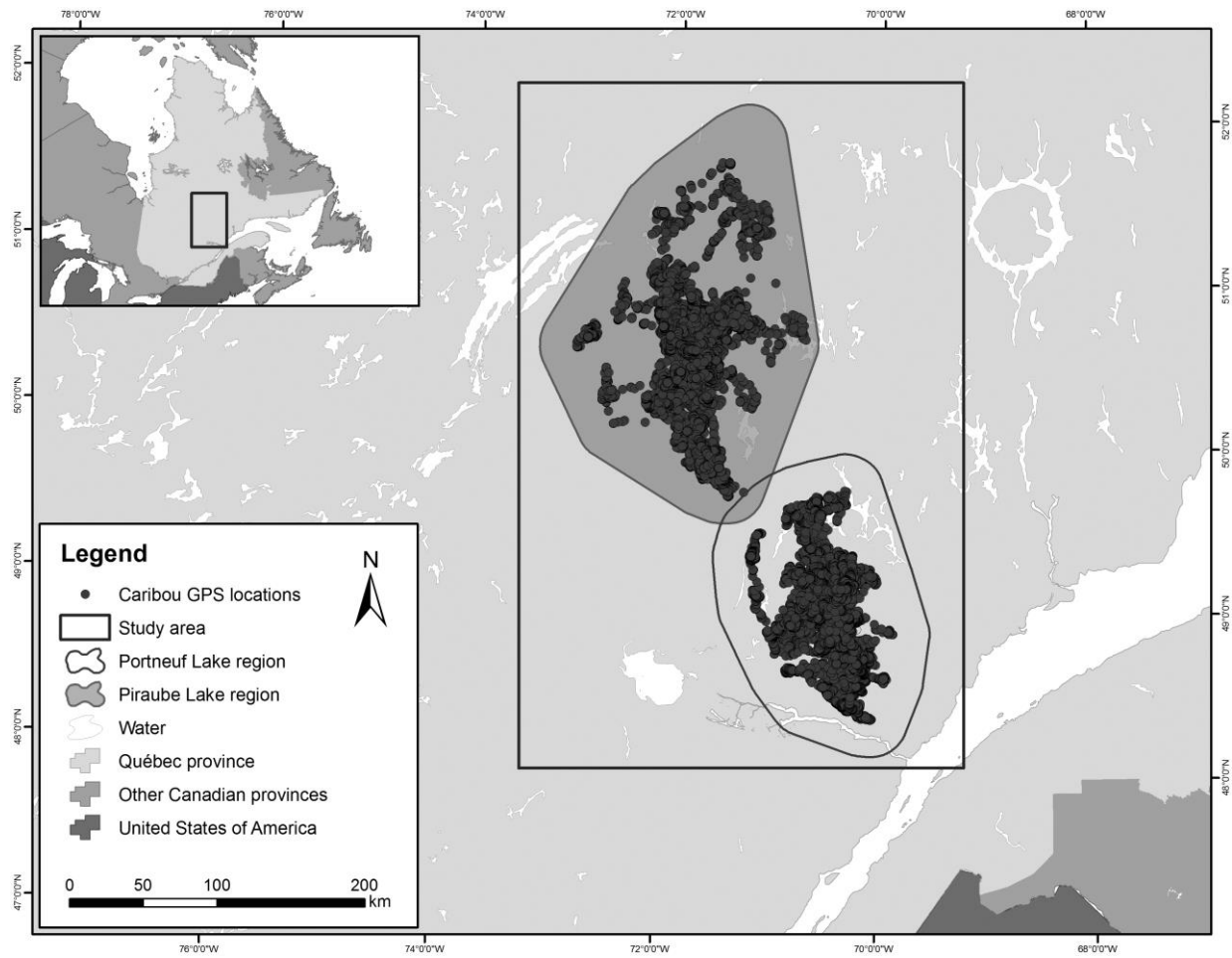
## FIGURE LEGENDS

**Fig. 1.**— Location of the study area in central Québec, Canada (upper-left insert) where we monitored 50 adult female caribou (*Rangifer tarandus caribou*) using GPS telemetry between 2004 and 2010. The delineation of the two parts of the study area (Piraube Lake in the North, Portneuf Lake in the south) is shown as well as the 288,665 GPS relocations used to calculate residency time using first-passage time analyses.

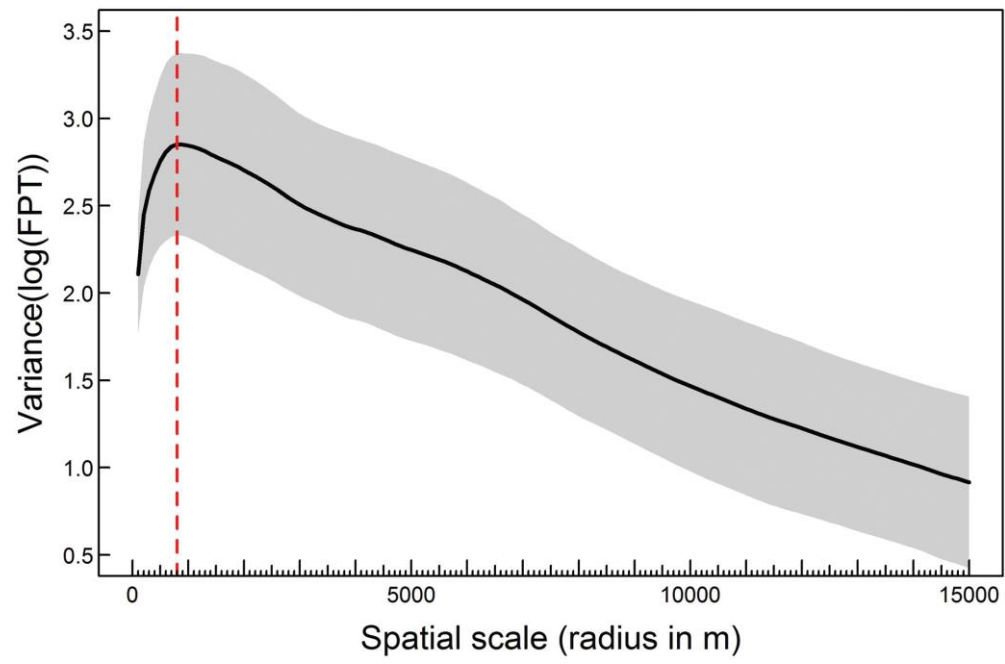
**Fig. 2.**— Observed variance in the natural log of residency time (first-passage time, FPT) of adult female caribou (*Rangifer tarandus caribou*) at various spatial scales. The continuous black line represents the mean  $\pm 1$  SD (shaded area), calculated on  $n = 51$  individual tracks that lasted for at least 6 months. The vertical dashed line indicates the spatial scale at which the maximum in variance is observed (800 m). Based on this preliminary analysis, we extracted environmental data using an 800 m buffer (cf. methods for the details).

**Fig. 3.**— Predictions (full line) and 95% CI (dashed lines) of road density (calving season), elevation (summer), and the proportion of coniferous stands (winter) of the most parsimonious models explaining residency time in a radius of 800 m of adult female caribou (*Rangifer tarandus caribou*) in Québec, Canada.

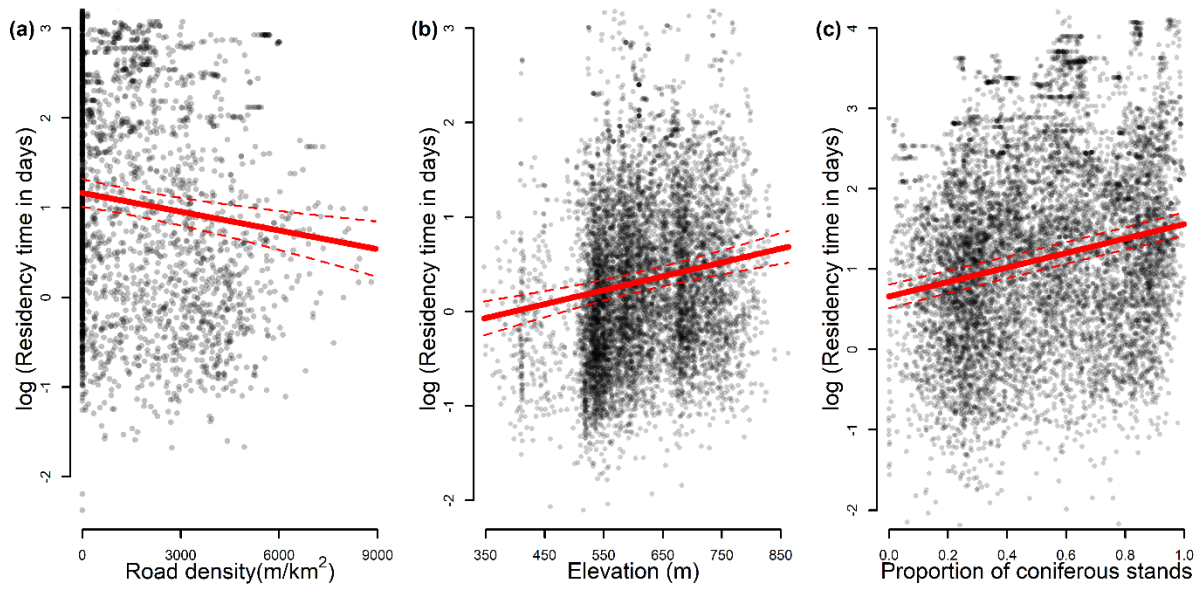
Figure 1



**Figure 2**



**Figure 3**





**Table 1.** Candidate models tested to determine if daily weather and disturbances influence residency time of female caribou (*Rangifer tarandus caribou*) in Québec, Canada. All candidate models included Year nested in individual identity as a random intercept.

<b>Model</b>	<b>Variables included</b>	<b>No. of parameters (k)</b>	<b>General biological interpretation – Movement patterns are mostly affected by:</b>
1	Intercept only	4	<i>No fixed factors considered here (null model)</i>
2	Precipitation + Temperature	6	Weather
3	Precipitation × Temperature	7	Weather
4	Clearcut 0-5 + Clearcut 6-20 + Road density	7	Disturbance
5	Coniferous stands + Elevation + Ruggedness <sup>a</sup>	7	Habitat
6	Model 2 + Model 4	9	Weather + Disturbance
7	Model 2 × Model 4	15	Weather interacting with Disturbance
8	Model 7 + Model 3	16	Weather interacting with Disturbance
9	Model 2 + Model 5	9	Weather + Habitat
10	Model 3 + Model 5	10	Weather + Habitat
11	Model 4 + Model 5	10	Disturbance + Habitat
12	Model 4 + Model 9	12	Disturbance + Weather + Habitat
13	Model 5 + Model 7	18	Habitat + Weather interacting with Disturbance
14	Model 3 + Model 13	19	Habitat + Weather interacting with Disturbance

<sup>a</sup> defined as the coefficient of variation of elevation

**Table 2.** Difference in AIC ( $\Delta$  AIC) to the top-ranked model (bold and underlined), AIC weight ( $\omega$ ) and deviance ( $d$ ) of the candidate models tested to determine if daily weather and disturbances influence residency time of adult female ( $n = 50$ ) caribou (*Rangifer tarandus caribou*) in Québec (Canada) at a radius of 800 m. See Table 1 for model description. Models with  $\Delta$ AIC < 2 were considered competitive and are shown in bold.

Model	Winter			Spring			Calving			Summer			Rut		
	$\Delta$ AIC	$\omega$	$d$	$\Delta$ AIC	$\omega$	$d$	$\Delta$ AIC	$\omega$	$d$	$\Delta$ AIC	$\omega$	$d$	$\Delta$ AIC	$\omega$	$d$
1	287.18	0.00	14893	43.26	0.00	4453	50.87	0.00	4918	84.82	0.00	11741	44.66	0.00	6361
2	279.52	0.00	14881	36.73	0.00	4442	51.43	0.00	4914	85.48	0.00	11737	39.41	0.00	6351
3	279.45	0.00	14879	35.77	0.00	4439	53.34	0.00	4914	86.69	0.00	11737	41.41	0.00	6351
4	248.79	0.00	14849	45.99	0.00	4450	26.73	0.00	4887	56.70	0.00	11707	28.23	0.00	6338
5	8.68	0.00	14608	9.60	0.01	4413	9.77	0.00	4871	15.37	0.00	11665	13.45	0.00	6323
6	239.86	0.00	14836	39.09	0.00	4439	26.84	0.00	4884	57.21	0.00	11703	22.27	0.00	6328
7	241.97	0.00	14826	45.02	0.00	4433	37.25	0.00	4882	64.07	0.00	11698	25.40	0.00	6319
8	242.23	0.00	14824	43.74	0.00	4429	39.13	0.00	4882	65.44	0.00	11697	27.37	0.00	6319
9	<b>0.04</b>	0.30	14596	<b>0.50</b>	0.43	4400	10.27	0.00	4867	16.51	0.00	11662	7.49	0.02	6313
10	<b><u>0.00</u></b>	0.31	14594	<b><u>0.00</u></b>	0.54	4398	12.21	0.00	4867	17.81	0.00	11662	9.49	0.01	6313
11	9.47	0.00	14603	15.29	0.00	4413	<b><u>0.00</u></b>	0.54	4855	<b><u>0.00</u></b>	0.59	11644	6.45	0.03	6310
12	<b>0.93</b>	0.19	14591	6.13	0.03	4400	<b>0.37</b>	0.45	4851	<b>0.78</b>	0.39	11641	<b><u>0.00</u></b>	0.71	6300
13	<b>1.90</b>	0.12	14580	11.88	0.00	4394	10.72	0.00	4849	7.41	0.01	11635	2.69	0.18	6291
14	2.57	0.08	14578	11.15	0.00	4391	12.63	0.00	4849	8.83	0.01	11635	4.67	0.07	6291

**Table 3.** Coefficients ( $\beta$ ) and 95% confidence intervals of the most parsimonious models explaining residency time of adult female ( $n = 50$ ) caribou (*Rangifer tarandus caribou*) in a radius of 800 m during winter and spring. Coefficients are scaled. Coefficients with 95% confidence intervals (Lower – Upper) that do not overlap 0 are in bold.

Variable	Winter			Spring		
	$\beta$	Lower	Upper	$\beta$	Lower	Upper
Intercept	<b>1.111</b>	<b>0.973</b>	<b>1.250</b>	<b>0.520</b>	<b>0.402</b>	<b>0.638</b>
Precipitation	0.006	-0.011	0.024	0.013	-0.017	0.043
Temperature	<b>-0.043</b>	<b>-0.070</b>	<b>-0.016</b>	<b>-0.115</b>	<b>-0.191</b>	<b>-0.040</b>
Coniferous	<b>0.232</b>	<b>0.204</b>	<b>0.260</b>	<b>0.047</b>	<b>0.000</b>	<b>0.094</b>
Elevation	<b>0.116</b>	<b>0.058</b>	<b>0.174</b>	0.022	-0.041	0.085
Ruggedness	0.016	-0.011	0.044	<b>0.106</b>	<b>0.072</b>	<b>0.140</b>
Precipitation x Temperature	0.013	-0.005	0.030	0.072	-0.017	0.160

**Table 4.** Coefficients ( $\beta$ ) and 95% confidence intervals of the most parsimonious models explaining residency time of adult female ( $n = 50$ ) caribou (*Rangifer tarandus caribou*) in a radius of 800 m during calving, summer, and rut. Coefficients are scaled. Coefficients with 95% confidence intervals (Lower – Upper) that do not overlap 0 are in bold.

Variable	Calving			Summer			Rut		
	$\beta$	Lower	Upper	$\beta$	Lower	Upper	$\beta$	Lower	Upper
Intercept	<b>0.97</b>	<b>0.82</b>	<b>1.12</b>	<b>0.30</b>	<b>0.19</b>	<b>0.40</b>	<b>0.48</b>	<b>0.39</b>	<b>0.57</b>
Precipitation							-0.01	-0.02	0.00
Temperature							<b>-0.09</b>	<b>-0.15</b>	<b>-0.02</b>
Clearcut 0-5	0.01	-0.04	0.05	-0.02	-0.04	0.00	<b>-0.05</b>	<b>-0.08</b>	<b>-0.01</b>
Clearcut 6-20	0.02	-0.07	0.11	-0.02	-0.07	0.03	0.00	-0.06	0.05
Road density	<b>-0.15</b>	<b>-0.23</b>	<b>-0.07</b>	<b>-0.06</b>	<b>-0.10</b>	<b>-0.02</b>	-0.04	-0.08	0.01
Coniferous	0.07	0.00	0.14	0.03	0.00	0.06	0.02	-0.02	0.06
Elevation	<b>0.17</b>	<b>0.08</b>	<b>0.26</b>	<b>0.14</b>	<b>0.09</b>	<b>0.19</b>	0.05	-0.01	0.12
Ruggedness	<b>0.10</b>	<b>0.06</b>	<b>0.14</b>	<b>0.08</b>	<b>0.05</b>	<b>0.11</b>	<b>0.09</b>	<b>0.05</b>	<b>0.13</b>

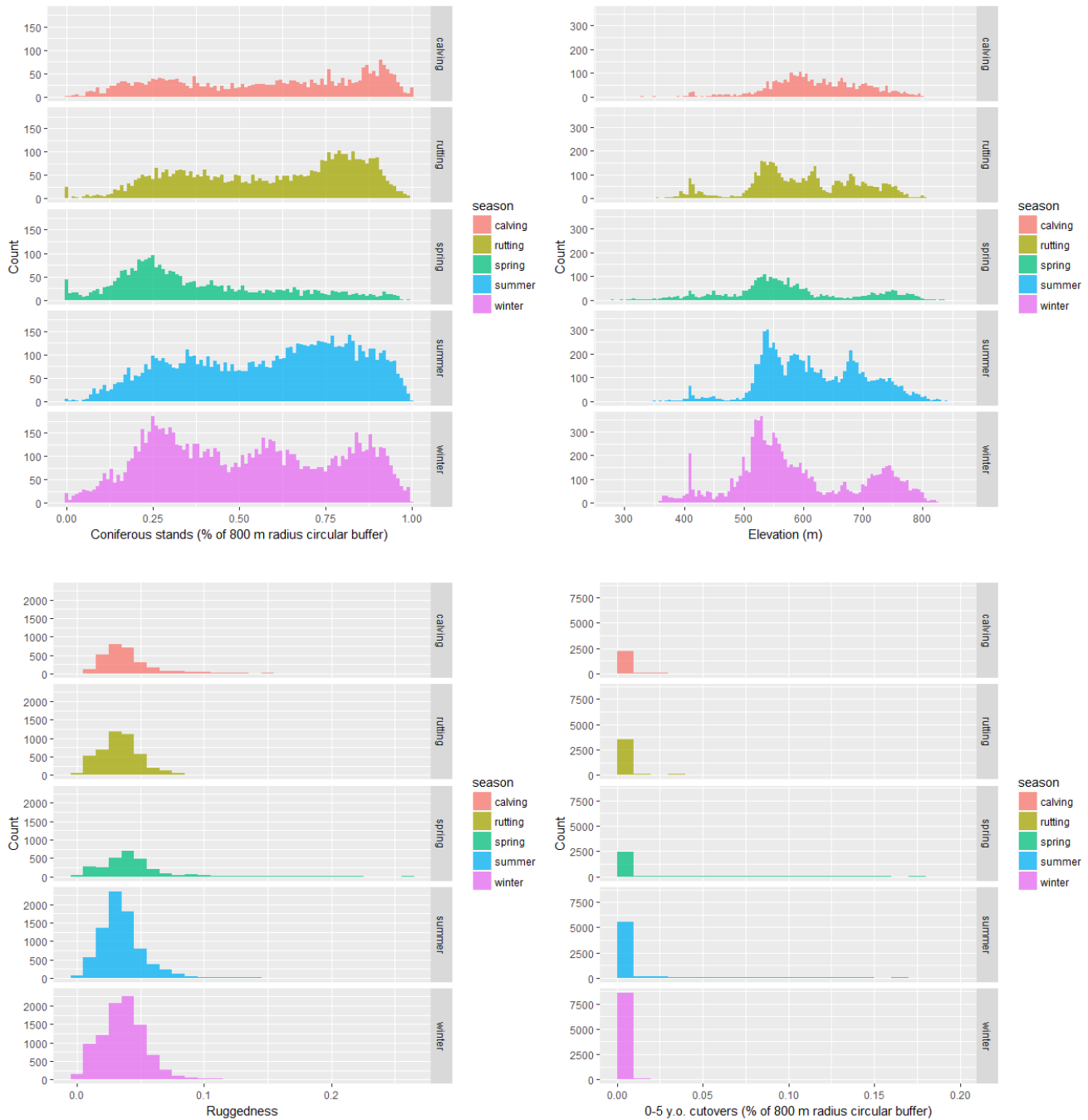
**Supplementary Data SD1.** Summary of the GPS tracking of 50 adult female caribou (*Rangifer tarandus caribou*). Some individuals were tracked for several non-consecutive periods (see column “bout”). The complete database yields a total of 70 bouts with a mean duration of 61.4 weeks (range = 6.3–223.9 weeks).

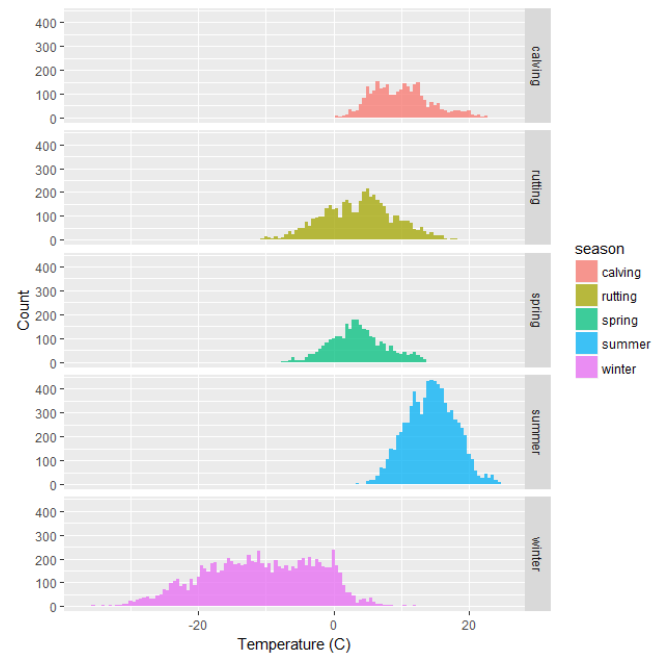
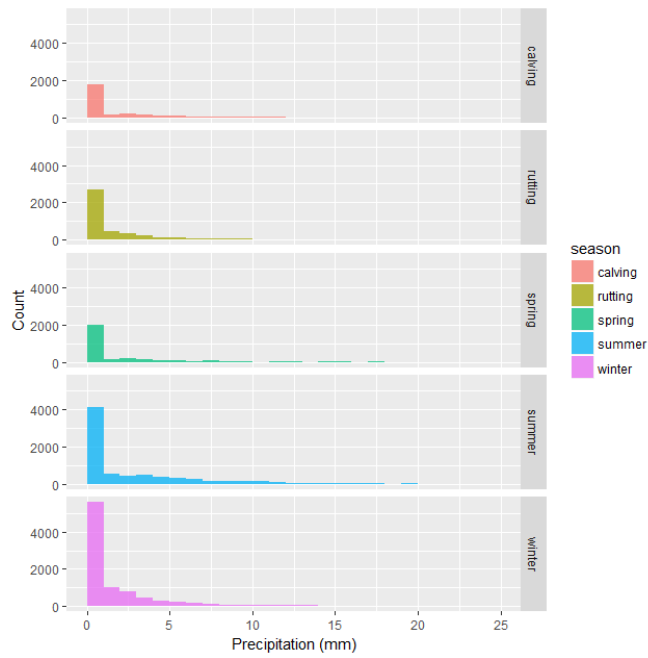
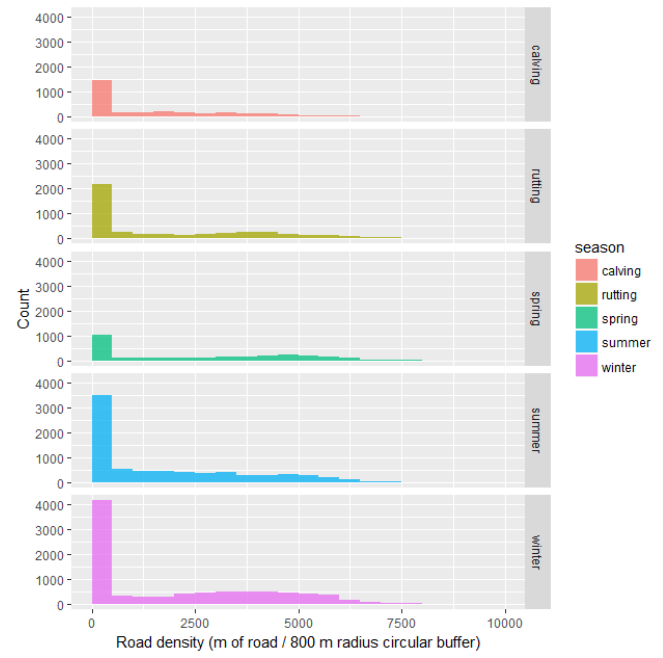
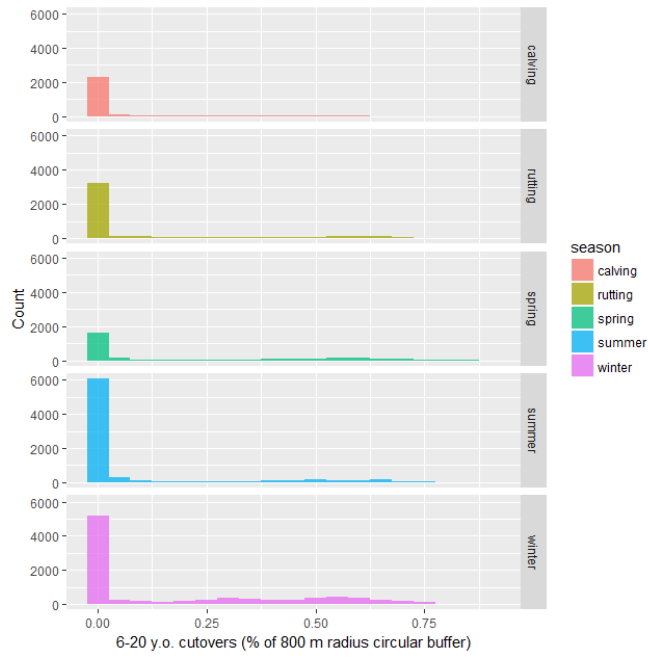
<b>Female ID</b>	<b>Bout</b>	<b>N</b>	<b>Start date</b>	<b>End date</b>	<b>Duration (weeks)</b>
F01	1	4412	2005-04-15	2007-09-21	127.0
F02	1	5479	2005-04-15	2008-02-20	148.8
F03	1	2005	2005-04-06	2006-03-16	49.1
F04	1	1975	2005-04-15	2006-03-15	47.8
F05	1	2090	2005-04-07	2006-03-15	48.9
F06	1	2017	2005-04-15	2006-03-15	47.8
F07	1	3837	2006-03-17	2008-02-27	101.8
F08	1	3771	2006-03-17	2008-03-10	103.4
F09	1	260	2006-03-16	2006-04-29	6.3
F10	1	7312	2010-02-01	2010-12-31	106.2
F11	1	6390	2008-03-25	2010-12-31	161.5
F12	1	362	2008-03-18	2008-05-29	10.3
F13	1	6275	2009-01-01	2010-12-31	122.0
F14	1	6799	2008-03-17	2010-12-31	202.0
F15	1	7543	2010-01-17	2010-12-31	108.4
F16	1	6739	2010-03-13	2010-12-31	98.4
F17	1	3703	2010-03-15	2010-12-31	54.4
F18	1	6984	2010-03-14	2010-12-31	100.4
F19	1	13235	2004-04-15	2007-04-01	154.5
F20	1	19208	2004-04-15	2008-07-30	223.9
F20	2	1363	2009-05-01	2010-01-30	39.3
F21	1	11497	2004-04-15	2006-06-20	113.7
F22	1	8724	2006-04-15	2009-03-11	151.7
F23	1	921	2006-03-06	2006-06-26	15.9
F24	1	867	2007-04-15	2007-07-30	15.1
F24	2	2017	2008-02-01	2009-03-10	57.7
F25	1	3366	2007-04-15	2008-02-29	45.8
F25	2	3895	2008-05-01	2010-06-25	112.1
F26	1	4159	2008-03-08	2009-03-12	52.8
F27	1	1712	2009-04-14	2010-03-09	47.1
F28	1	642	2010-03-11	2010-07-13	17.7
F29	1	2209	2004-04-15	2004-12-09	34.1
F29	2	2083	2006-03-12	2006-06-30	15.6
F30	1	3880	2004-04-15	2005-03-17	48.1
F31	1	964	2004-03-17	2004-06-09	12.0
F32	1	924	2004-04-15	2004-10-14	26.1

F32	2	3906	2005-03-04	2006-02-19	50.4
F32	3	5276	2007-04-03	2007-11-29	34.4
F33	1	1840	2004-03-17	2004-09-01	24.0
F34	1	8042	2004-04-15	2006-05-31	110.8
F35	1	1399	2004-04-15	2004-08-30	19.6
F35	2	6807	2004-11-01	2005-11-21	55.0
F36	1	7028	2004-04-15	2005-03-01	45.7
F36	2	4566	2007-04-15	2007-10-31	28.4
F37	1	1315	2004-03-17	2004-07-08	16.1
F38	1	1768	2004-04-15	2004-10-01	24.1
F38	2	2970	2004-12-15	2005-10-03	41.7
F38	3	7615	2005-10-18	2007-01-31	67.1
F39	1	12927	2004-04-15	2006-07-26	118.9
F39	2	6257	2007-07-12	2008-03-31	37.6
F40	1	19280	2004-04-15	2006-10-01	128.4
F40	2	3447	2007-04-03	2007-08-31	21.5
F41	1	2815	2004-04-15	2005-02-22	44.8
F41	2	3030	2006-03-15	2006-08-20	22.6
F41	3	3438	2007-04-04	2008-03-09	48.7
F42	1	976	2004-04-15	2004-07-20	13.8
F42	2	862	2005-03-03	2005-06-02	13.1
F43	1	1582	2004-04-15	2004-09-01	19.8
F43	2	3218	2004-12-15	2005-09-21	39.9
F44	1	15631	2005-07-01	2007-10-31	121.7
F44	2	4016	2008-03-11	2009-03-11	52.3
F44	3	1298	2009-04-15	2010-01-09	38.5
F45	1	3768	2006-04-15	2006-10-10	25.4
F45	2	4738	2007-04-03	2007-11-01	30.3
F46	1	1093	2005-04-15	2005-07-21	13.8
F46	2	2138	2005-08-31	2006-03-11	27.6
F47	1	3714	2007-04-15	2007-11-01	28.6
F48	1	1694	2008-09-21	2009-03-09	24.3
F49	1	3288	2008-03-13	2009-01-14	43.9
F50	1	2953	2009-04-14	2010-01-13	39.2

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**Supplementary Data SD2.** Distribution of values for each variable in the dataset used to determine residency time (first passage time) at 800 m in adult female caribou (*Rangifer tarandus caribou*). Please note that the distribution shows the raw value, not the scaled values used in the statistical analyses.







**Supplementary Data SD3.** Variance explained (%) by fixed and random effects in the most parsimonious model describing residency time (first passage time) at 800 m for each biological period.

	<b>Winter</b>	<b>Spring</b>	<b>Calving</b>	<b>Summer</b>	<b>Rutting</b>
Variance explained by fixed effects	3.61	3.38	3.21	3.34	1.66
Variance explained by caribou ID	5.70	1.66	<0.01	7.04	2.54
Variance explained by Year nested within ID	10.14	15.66	<0.01	11.81	6.11
Total variance explained	19.45	20.70	3.21	22.18	10.31

**Supplementary Data SD4.** Relative importance of each variable for each biological period in explaining residency time (first passage time) at 800 m for caribou (*Rangifer tarandus caribou*) in Canada. We calculated the relative importance of each predictor variable using the MuMIn package (Barton 2018) in R 3.4.3 (R Development Core Team 2017).

<b>Variable</b>	<b>Winter</b>	<b>Spring</b>	<b>Calving</b>	<b>Summer</b>	<b>Rutting</b>
Clearcut 0-5	0.39	0.03	0.99	1.00	0.98
Clearcut 6-20	0.39	0.03	0.99	1.00	0.98
Road density	0.39	0.03	0.99	1.00	0.98
Coniferous	1.00	1.00	1.00	1.00	1.00
Elevation	1.00	1.00	1.00	1.00	1.00
Ruggedness	1.00	1.00	1.00	1.00	1.00
Precipitation	0.99	1.00	0.45	0.42	0.97
Temperature	0.99	1.00	0.45	0.42	0.97
Precipitation x Clearcut 0-5	0.20	<0.01	<0.01	0.02	0.24
Precipitation x Clearcut 6-20	0.20	<0.01	<0.01	0.02	0.24
Precipitation x Road density	0.20	<0.01	<0.01	0.02	0.24
Temperature x Clearcut 0-5	0.20	<0.01	<0.01	0.02	0.24
Temperature x Clearcut 6-20	0.20	<0.01	<0.01	0.02	0.24
Temperature x Road density	0.20	<0.01	<0.01	0.02	0.24
Precipitation x Temperature	0.39	0.54	<0.01	<0.01	0.07