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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 6th 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 km² (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 ± 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; Beaudesne 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 *Daily weather data.*— Daily weather data were produced by Natural Resources Canada and
176 interpolated at a spatial resolution of 10 km. Daily gridded values of temperature and total precipitation
177 were extracted for the years 2004-2010 for our study region, based on the methodology described in
178 Hutchinson et al. (2009) and Hopkinson et al. (2011). We extracted mean daily temperature and
179 precipitation values at each GPS relocation.

180 *Residency time assessed using first-passage time.*— We used a two-step approach based on first
181 passage time (FPT) analysis (Fauchald and Tveraa 2003) to estimate the time spent by an individual in
182 an area. FPT is a measure of the time used by an individual to cross a circle of given radius (scale), and
183 is thus related to residency time. In a first exploratory step, we aimed at obtaining a general picture of
184 the spatial scales at which individuals of our study population were using their habitat. We recalculated
185 the positions along the tracks at 100-m intervals using the method provided by (“rediscretizing”;
186 Calenge 2006) and then calculated the variance of the natural log in FPT [$var(\log(\text{FPT}))$], following
187 Fauchald and Tveraa (2003). FPT was calculated over a sequence of spatial scales with radii ranging
188 from 100 to 15,000 m, using 100-m increasing intervals. Only tracks that covered more than 6 months
189 of consecutive tracking ($n = 51$ out of the 70 tracks) were used in this first step to avoid using tracks
190 that would represent only a very short period of the annual cycle. The results were then averaged to
191 investigate the occurrence of peaks in $var(\log(\text{FPT}))$, indicative of spatial scales at which area-
192 restricted search behavior takes place. We observed a peak in variance at 800 m (Fig. 2) and this spatial
193 scale was used in subsequent analysis.

194 In a second step, we calculated FPT (in days) at each actual GPS relocation within a circle of
195 radius (scale) of 800 m using the complete set of tracks ($n = 70$, see Supplementary Data SD1). Habitat
196 and weather covariates were extracted over circular areas with a radius of 800 m centered on each

197 relocation. Relocations for which environmental or habitat data were not available were removed from
198 the datasets. In addition, FPT cannot be estimated at the beginning and end of any given track for a
199 number of relocations. This resulted in a final sample size of 288,665 GPS relocations, with an average
200 of 5,773 relocations per individual.

201 We processed all movement data using R 3.2.3 (R Development Core Team 2017). We used the
202 *adehabitatLT* package v.0.3.16 (Calenge 2006) for FPT calculations. We extracted environmental data
203 using the Geospatial Modelling Environment v.0.2.7.0 (Beyer 2012), which uses ArcGIS v.10.0 (ESRI
204 2011) as the computation engine.

205 *Statistical analyses.*— We used daily average of FPT to reduce pseudo-replication and to
206 compensate for slightly different sampling rates among individuals. We log-transformed daily average
207 of FPT to fulfill all statistical assumptions. We modeled variation in $\log(\text{FPT})$ of caribou using linear
208 mixed-effects models with the *nlme* package (Pinheiro et al. 2018) in R 3.4.3 (R Development Core
209 Team 2017). We controlled for repeated measures by adding individual identity (ID) as a random
210 intercept and we added Year nested within ID to handle individual variation among years. We also
211 controlled for temporal autocorrelation by adding a first order autocorrelation structure in the model
212 specifications (Crawley 2007; Pinheiro et al. 2018). Using Akaike's information criterion (AIC;
213 Burnham and Anderson 2002), we evaluated, for each biological period separately, a set of 14 plausible
214 candidate models (Table 1) that combined different additive and interactive effects of continuous
215 variables describing daily weather (temperature, precipitation), disturbances (proportion of 0-5-years-
216 old clearcuts, proportion of 6-20-years-old clearcuts, road density), and natural habitat types
217 (proportion mature coniferous stands, elevation, terrain ruggedness). The candidate models
218 corresponded to different biological interpretations linked to our hypothesis (Table 1). Given that the

219 14 candidate models were constructed hierarchically, we selected the most parsimonious per biological
220 period using AIC and we did not perform model-averaging (Arnold 2010). Models with $\Delta AIC < 2$ were
221 considered competitive. We calculated the relative importance of each predictor variable with the
222 *MuMin* package (Barton 2018) and we calculated, for the most parsimonious model, the proportion of
223 variance explained by fixed and random effects based on Nakagawa and Schielzeth (2013). We scaled
224 (mean = 0, variance = 1) all predictor variables for easier model convergence (see Supplementary Data
225 SD2 for raw distribution and the units of variables). Variance inflation factor for the most parsimonious
226 models were < 3 (Graham 2003) and we examined the residuals visually to confirm the absence of a
227 clear deviation from normality.

228

229

RESULTS

230 From the set of 14 candidate models tested, three were retained as competitive for at least one of
231 the five periods (Table 2). Natural habitat types (coniferous forest, elevation, ruggedness) were retained
232 in the top-ranked model in all biological periods (Table 2). The top-ranked model also included the
233 effects of disturbances (clearcuts and roads) during calving, summer, and rut, while daily weather
234 variables were retained in the top-ranked model during winter, spring, and rut, as well as the most
235 competitive models during winter and spring. The synergistic effects of human disturbances and daily
236 weather were not retained in any biological periods ($\Delta AIC = 1.90 - 11.15$; Table 2). Total variance,
237 i.e., including fixed and random effects, explained by the most parsimonious models ranged from 3.2%
238 (calving) to 22.2% (summer; Supplementary Data SD3).

239

240

Some general patterns emerged across biological periods. First, daily weather influenced FPT.

We observed a decrease in FPT with increasing temperature during winter, spring, and rut, but we

241 found no evidence for any effect of precipitation (Tables 3-4). Second, disturbances also influenced
242 FPT, which decreased with increasing road density and greater proportion of young (0-5-years-old)
243 clearcuts during calving, summer, and rut (Table 4). Finally, our results showed that variables
244 considered in the model based on natural habitat types influenced FPT: higher elevation and more
245 rugged terrain increased FPT in most biological periods, and greater proportion of mature coniferous
246 stands increased FPT during winter and spring (Tables 3-4, Fig. 3). Effect sizes (Tables 3-4) and the
247 relative importance (Supplementary Data SD4) of the predictor variables in the models suggest that
248 natural habitat types were the main factor influencing FPT, while the importance of daily weather and
249 disturbances on FPT were not consistent across periods. Daily weather was more important during
250 winter and spring, while disturbances were more important during calving and summer.

251

252

DISCUSSION

253 Most previous studies on movement and space-use patterns in terrestrial mammals investigated the
254 effects of disturbed habitat types and linear features such as roads (e.g., Prokopenko et al. 2017;
255 Monteith et al. 2018). Although some of those studies attempted to control for weather by dividing
256 annual data into different biological periods (e.g., Leblond et al. 2010; van Beest et al. 2013), the
257 effects of fine-scale variation in daily weather within a biological period has rarely been investigated
258 (but see e.g., Monteith et al. 2011; Middleton et al. 2013). Here, we showed that residency time (i.e.
259 FPT) increased with colder weather and decreasing human disturbances. Those relationships, however,
260 did not hold in all biological periods. Disturbances had a larger effect on residency time than daily
261 weather during calving and summer, but this was reversed during winter and spring. Therefore, our
262 results only partially supported our prediction that daily weather would have a weaker effect than

263 habitat disturbances on residency time. Our results highlight the importance of studying animal
264 behavior over complete annual cycles as the effects of weather and disturbances on the movement may
265 vary seasonally. Finally, we found no evidence that residency time in disturbed habitats was modulated
266 by daily weather in our study system.

267 Herbivore movement behavior serves several purposes, including finding food resources,
268 avoiding predators, and finding shelter (Dussault et al. 2004; Leclerc et al. 2012b; Merkle et al. 2016).
269 Our results suggest that movements of caribou likely aim to reduce predation risk. By increasing
270 residency time in mature coniferous stands, at higher elevation, and in rugged terrain, caribou can
271 decrease the rate of encounters with predators such as wolves (*Canis lupus*), which usually use lower
272 elevations and flat terrain (Whittington et al. 2011; Lesmerises et al. 2012). Also, caribou tend to
273 reduce residency time with increasing road density. The presence of roads is associated with higher
274 encounter rate and predation risk by wolves (James and Stuart-Smith 2000; Whittington et al. 2011),
275 and roadsides are highly productive environments that are also selected by other predators of caribou
276 such as black bears (*Ursus americanus*), particularly during budbreak in spring and summer (Bastille-
277 Rousseau et al. 2011). Avoidance of human disturbances, especially roads, during calving has been
278 shown for boreal caribou in Québec (Leclerc et al. 2012b). Avoidance of disturbed habitat by females
279 with calves is known to increase their reproductive success (Leclerc et al. 2014) and likely have
280 impacts at the population level because calf survival can greatly influence population dynamics
281 (Gaillard et al. 2000). Our results are in line with previous work on boreal caribou that suggests that the
282 current recession of the southern limit of this threatened species is linked to anthropogenic disturbances
283 (Schaefer 2003; Vors et al. 2007) via maladaptive behavioral responses (Leclerc et al. 2014; Losier et
284 al. 2015; Lafontaine et al. 2017). Anthropogenic disturbances reduce the area of their prime habitat and

285 trigger the numerical and functional responses of alternative prey and predators (Seip 1992; Wittmer et
286 al. 2005; Courtois et al. 2008; DeCesare et al. 2010). Reduction of residency time in disturbed
287 landscape and in areas with higher predation risk was also observed in elk (*Cervus elaphus*). Indeed,
288 elk reduce their rate of movement and increase their residency time when hunter access (mainly roads)
289 is limited and when the occurrence of predators is lower (Frair et al. 2005; Cleveland 2012).

290 The strongest negative effect of road density and the strongest positive effects of elevation and
291 terrain ruggedness were observed during calving and summer: both variables are associated with an
292 increased avoidance of predation risk. Calving and summer are the most critical periods for female
293 reproductive success as the calves are highly vulnerable to predation (Pinard et al. 2012; Leclerc et al.
294 2014). In addition, all females showed similar behavioral responses to natural habitat types and human
295 disturbances during calving, as shown by the very low variance explained by random effects
296 (Supplementary SD3). We consider that natural selection may have shaped such behavioral responses
297 during this critical phase. In contrast, the higher individual variation in movement behavior measured
298 during other biological periods could indicate that appropriate responses to human disturbances and
299 adverse weather conditions can be achieved through different tactics that maintain phenotypic
300 variation. However, further studies will be necessary to confirm this hypothesis, and would for instance
301 involve measurements of indices of individual state (e.g., body mass, stress hormone levels) and fitness
302 (e.g., calf survival).

303 Individual variation in residency time could be due to differences in individual state, age, or
304 personality (Réale et al. 2010; Sih et al. 2015). While we controlled for daily weather, some variation
305 across and within years could be explained by other environmental variables related to daily weather
306 that were not included in this study, such as snow depth or temporary summer drought (Vandal and

307 Barrette 1985). Daily weather can influence the phenology of insects' emergence, snow and ice
308 melting, or rain-on-snow events, which in return could also modulate animal movement (Putkonen and
309 Roe 2003; Stien et al. 2010; Loe et al. 2016; Leblond et al. 2016b).

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

324 By combining daily weather variables and habitat disturbances in the same models, we showed
325 that their effects on residency time were additive. The absence of synergistic effects between habitat
326 disturbances and daily weather on residency time in our study may be explained by the low variability
327 of habitat disturbances at the spatial scale we conducted our analysis. Low variability in habitat

328 disturbances at an 800-m scale is expected in caribou as they tend to avoid human disturbances at much
329 larger spatial scales (Leclerc et al. 2012b; Leblond et al. 2013a; Fortin et al. 2013).

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

341

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356

357

SUPPLEMENTARY DATA

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359

360 **Supplementary Data SD1.**— Summary of the GPS tracking of 50 adult female caribou (*Rangifer*
361 *tarandus caribou*). Some individuals were tracked for several non-consecutive periods (see column
362 “bout”). The complete database yields a total of 70 bouts with a mean duration of 61.4 weeks (range =
363 6.3–223.9 weeks).

364

365 **Supplementary Data SD2.**— Distribution of values for each variable in the dataset used to determine
366 residency time (first-passage time) within a radius of 800 m in adult female caribou (*Rangifer tarandus*
367 *caribou*). Please note that the distribution shows the raw values, not the scaled values used in the
368 statistical analyses.

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370 **Supplementary Data SD3.**— Variance explained (%) by fixed and random effects in the most
371 parsimonious model describing residency time (first-passage time) within a radius of 800 m for each
372 biological period.

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374 **Supplementary Data SD4.**— Relative importance of each variable for each biological period in
375 explaining residency time (first-passage time) within a radius of 800 m for caribou (*Rangifer tarandus*
376 *caribou*) in Canada. We calculated the relative importance of each predictor variable using the MuMIn
377 package (Barton 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 first-passage times.

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 ± 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.

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.

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

^a defined as the coefficient of variation of elevation

Table 2. Difference in AIC (Δ AIC) to the most parsimonious models (in bold) 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.

Model	Δ AIC				
	Winter	Spring	Calving	Summer	Rut
1	287.18	43.26	50.87	84.82	44.66
2	279.52	36.73	51.43	85.48	39.41
3	279.45	35.77	53.34	86.69	41.41
4	248.79	45.99	26.73	56.70	28.23
5	8.68	9.60	9.77	15.37	13.45
6	239.86	39.09	26.84	57.21	22.27
7	241.97	45.02	37.25	64.07	25.40
8	242.23	43.74	39.13	65.44	27.37
9	0.04	0.50	10.27	16.51	7.49
10	0.00	0.00	12.21	17.81	9.49
11	9.47	15.29	0.00	0.00	6.45
12	0.93	6.13	0.37	0.78	0.00
13	1.90	11.88	10.72	7.41	2.69
14	2.57	11.15	12.63	8.83	4.67

Table 3. Coefficients (β) 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		
	β	Lower	Upper	β	Lower	Upper
Intercept	1.111	0.973	1.250	0.520	0.402	0.638
Precipitation	0.006	-0.011	0.024	0.013	-0.017	0.043
Temperature	-0.043	-0.070	-0.016	-0.115	-0.191	-0.040
Coniferous	0.232	0.204	0.260	0.047	0.000	0.094
Elevation	0.116	0.058	0.174	0.022	-0.041	0.085
Ruggedness	0.016	-0.011	0.044	0.106	0.072	0.140
Precipitation : Temperature	0.013	-0.005	0.030	0.072	-0.017	0.160

Table 4. Coefficients (β) 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		
	β	Lower	Upper	β	Lower	Upper	β	Lower	Upper
Intercept	0.97	0.82	1.12	0.30	0.19	0.40	0.48	0.39	0.57
Precipitation							-0.01	-0.02	0.00
Temperature							-0.09	-0.15	-0.02
Clearcut 0-5	0.01	-0.04	0.05	-0.02	-0.04	0.00	-0.05	-0.08	-0.01
Clearcut 6-20	0.02	-0.07	0.11	-0.02	-0.07	0.03	0.00	-0.06	0.05
Road density	-0.15	-0.23	-0.07	-0.06	-0.10	-0.02	-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	0.17	0.08	0.26	0.14	0.09	0.19	0.05	-0.01	0.12
Ruggedness	0.10	0.06	0.14	0.08	0.05	0.11	0.09	0.05	0.13

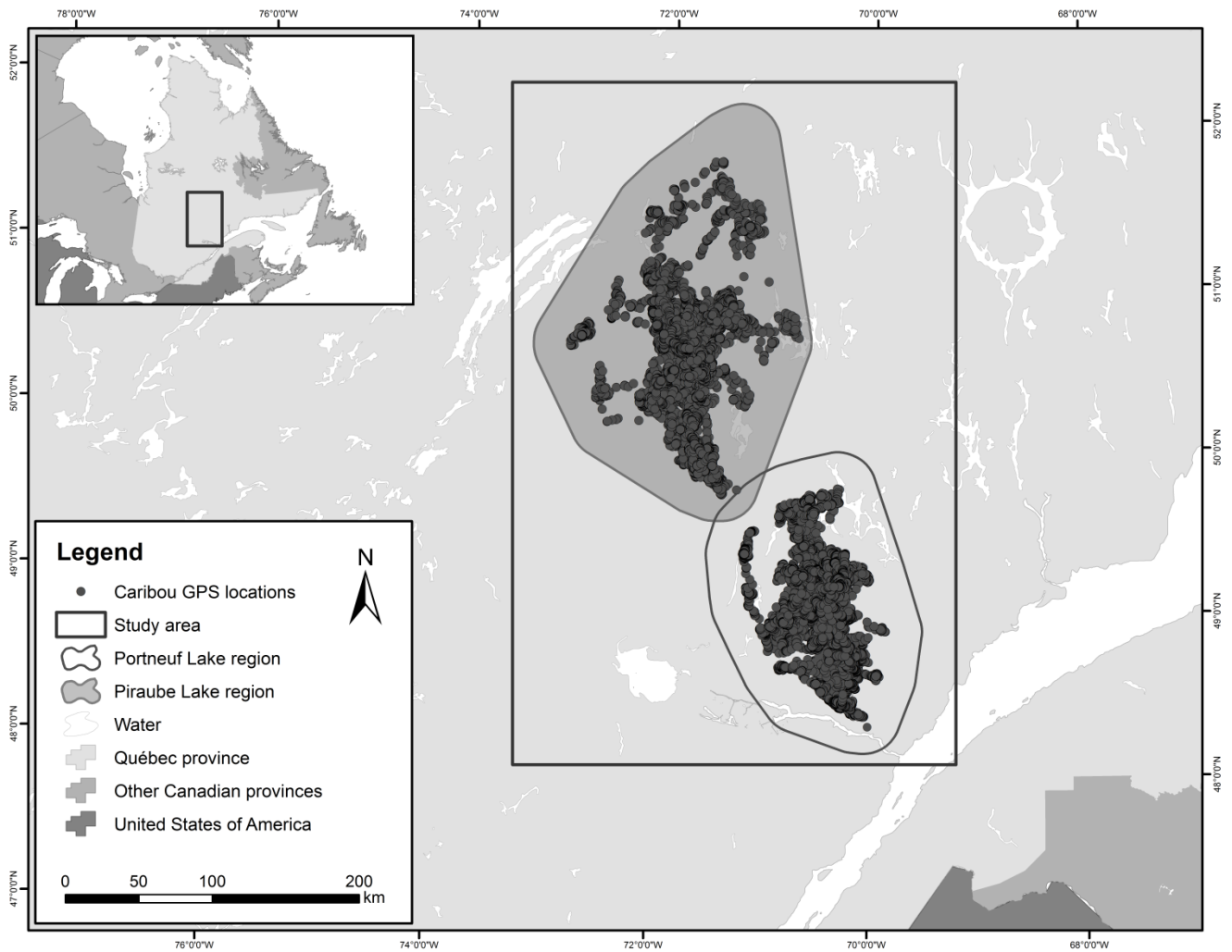


Fig. 1.

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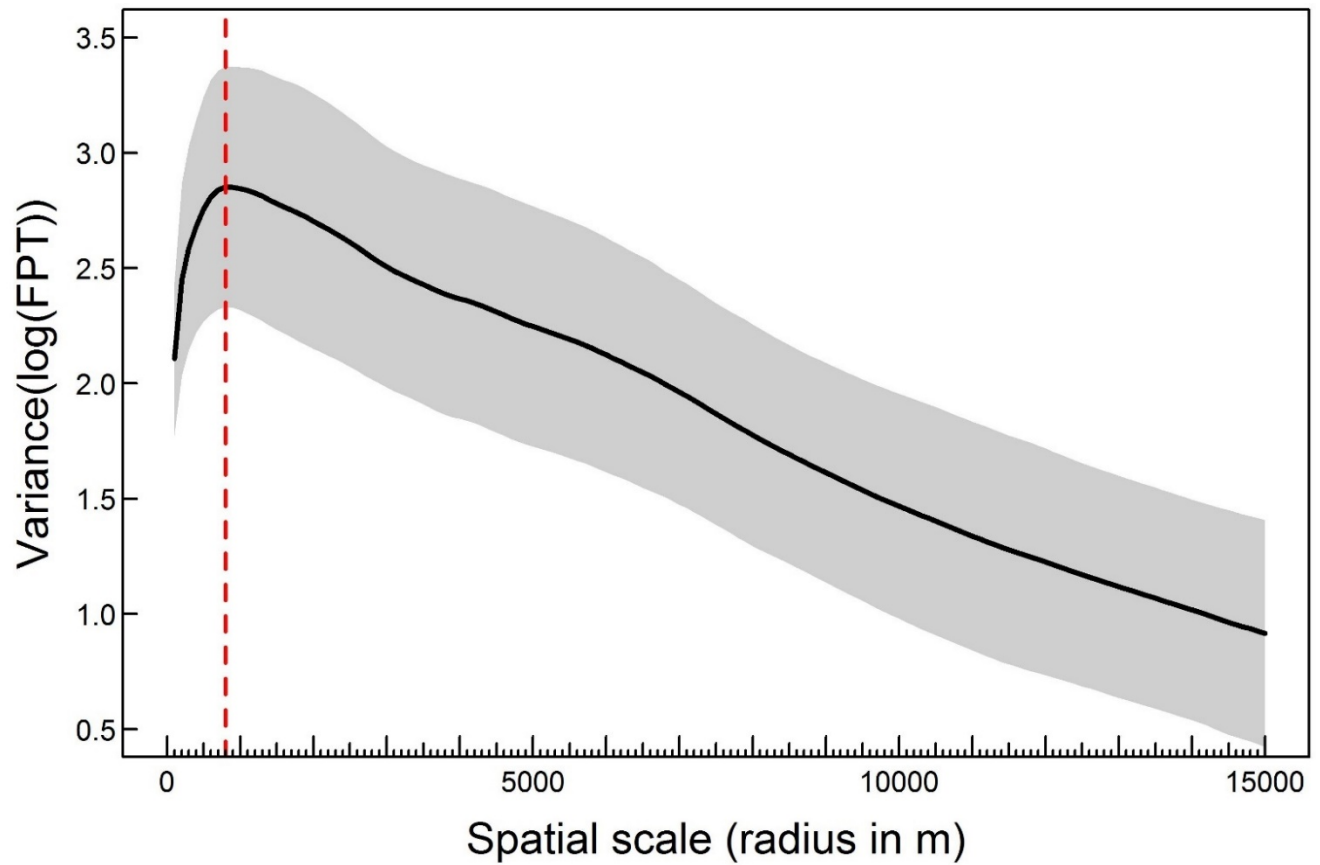


Fig. 2

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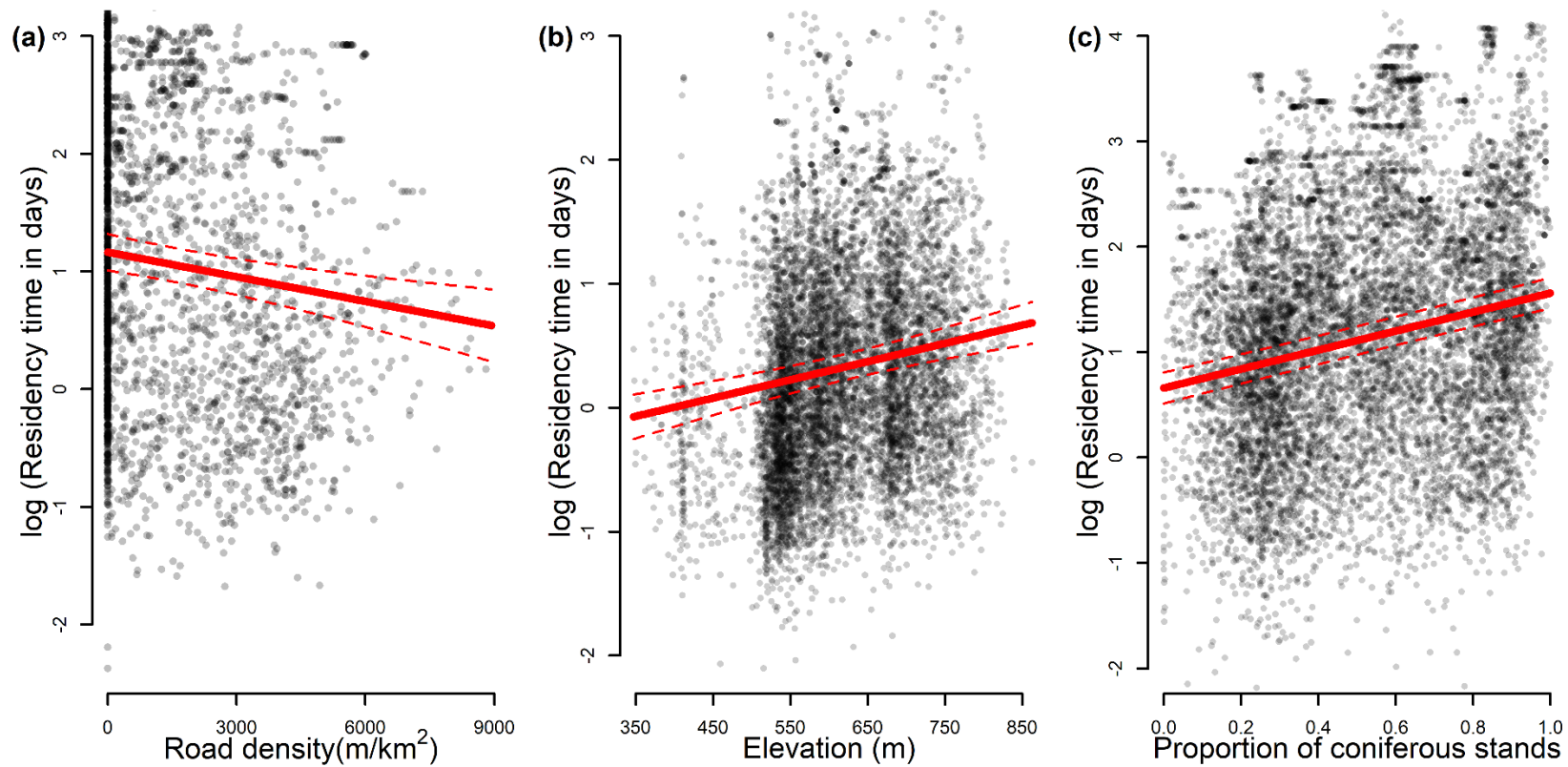


Fig. 3.

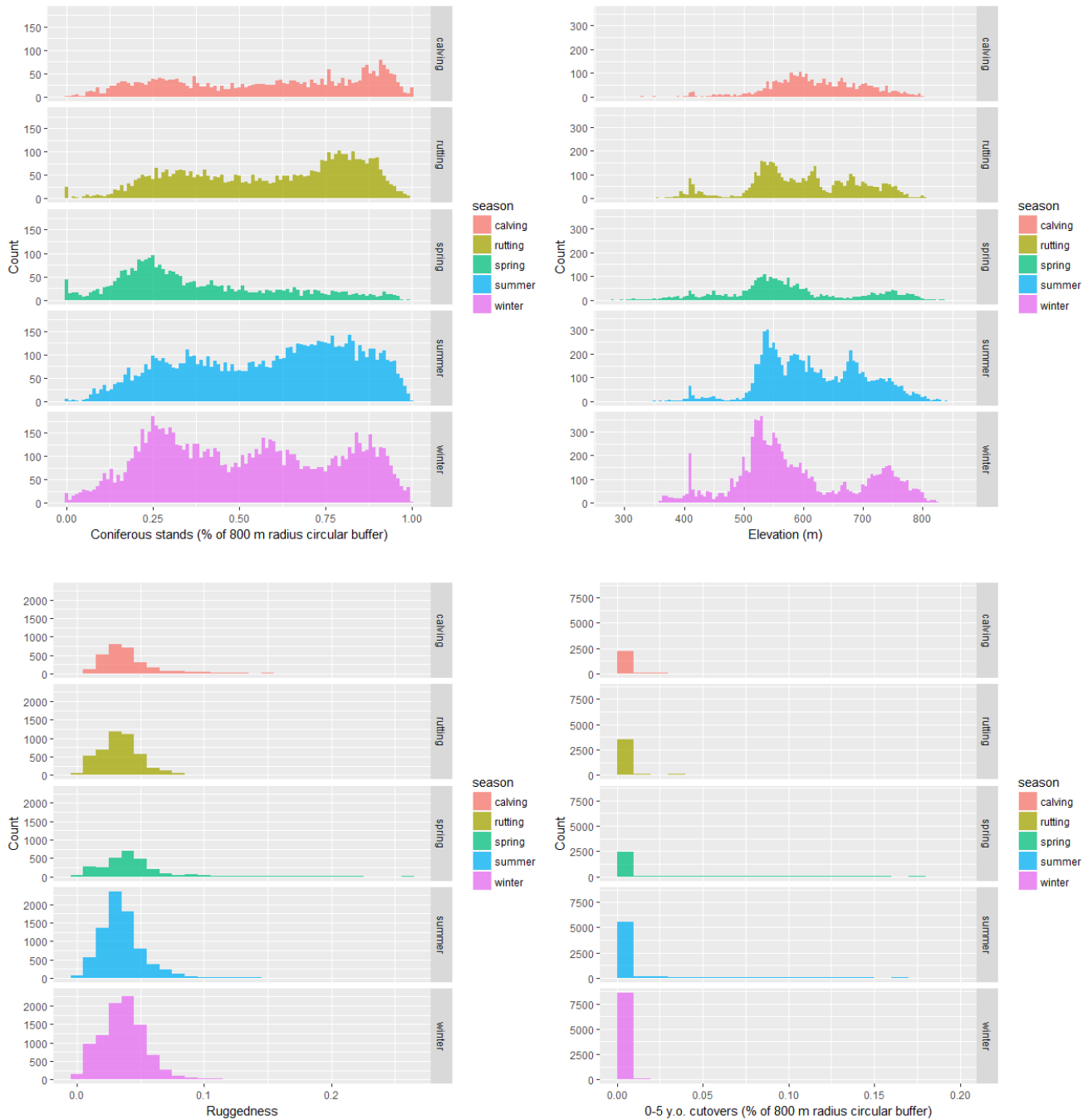
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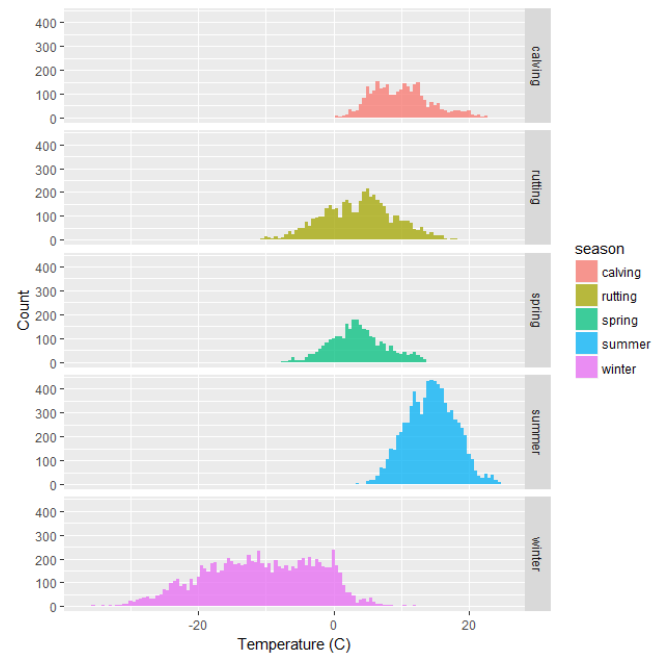
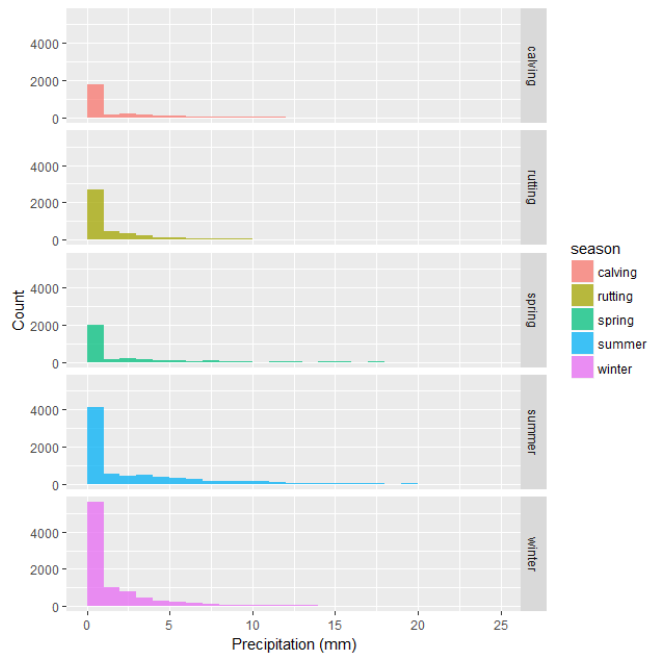
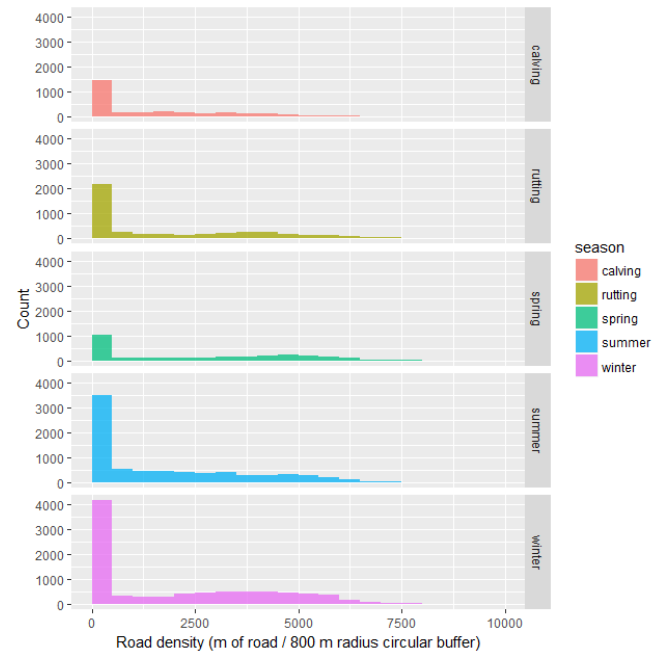
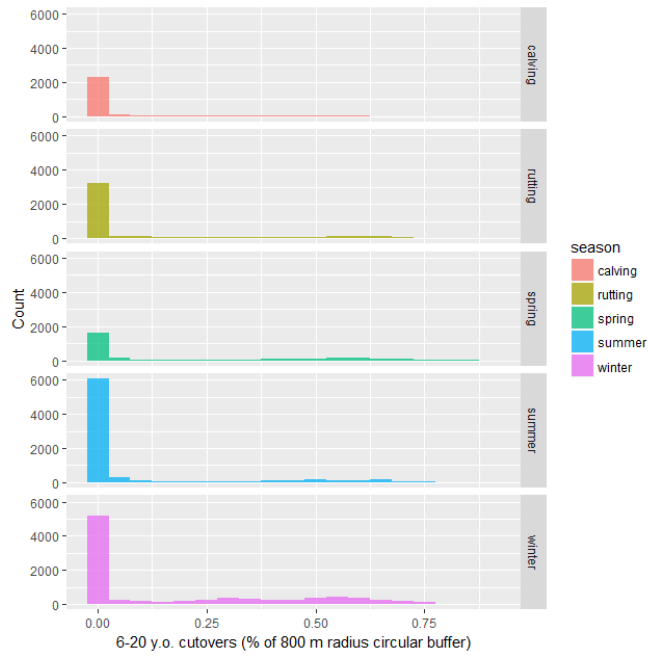
Supplementary Data SD1. Summary of the GPS tracking of 50 adult female caribou (*Rangifer tarandus caribou*). Some individuals were tracked for several non-consecutive periods (see column “bout”). The complete database yields a total of 70 bouts with a mean duration of 61.4 weeks (range = 6.3–223.9 weeks).

Female ID	Bout	N	Start date	End date	Duration (weeks)
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

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.

	Winter	Spring	Calving	Summer	Rutting
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).

Variable	Winter	Spring	Calving	Summer	Rutting
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 : Clearcut 0-5	0.20	<0.01	<0.01	0.02	0.24
Precipitation : Clearcut 6-20	0.20	<0.01	<0.01	0.02	0.24
Precipitation : Road density	0.20	<0.01	<0.01	0.02	0.24
Temperature : Clearcut 0-5	0.20	<0.01	<0.01	0.02	0.24
Temperature : Clearcut 6-20	0.20	<0.01	<0.01	0.02	0.24
Temperature : Road density	0.20	<0.01	<0.01	0.02	0.24
Precipitation : Temperature	0.39	0.54	<0.01	<0.01	0.07