Effects of human-induced disturbances and weather on herbivore movement

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

Key words: boreal forest, climate, first-passage time, GPS-tracking, habitat use, Rangifer tarandus caribou, residency time, ungulate

Earth has now entered its 6th mass extinction of species and human activities are at the center of this biodiversity crisis (Ceballos et al. 2015; Sánchez-Bayo and Wyckhuys 2019). Human-induced habitat loss and climate change modify environmental conditions and influence the abundance and distribution of species as well as the structure of communities (Schmiegelow and Mönkkönen 2002; Fahrig 2003; Williams and Jackson 2007). The way disturbances affect species–habitat relationships (Bachand et al. 2014), population dynamics (Laliberté and Ripple 2004), community structure (Williams et al. 2008; Velásquez-Tibatá et al. 2013), and intraspecific and interspecific interactions (Muhly et al. 2011; Steyaert et al. 2016) is of critical importance. Quantifying the effects of human disturbances on wildlife will allow predicting more efficiently the consequences of future environmental conditions on biodiversity.
Wildlife–habitat relationships can be studied by looking at behavioral traits, such as space use and movement of individuals on the landscape. For instance, recent studies suggest that human disturbances, such as roads, generally reduce movement and may even disrupt animal migrations (Seidler et al. 2015; Bauduin et al. 2018; Tucker et al. 2018). Considering that movements within and among seasonal ranges follow a strategy to minimize costs while maximizing access to high-quality resources (i.e., optimal foraging strategy—MacArthur and Pianka 1966; Schoener 1971; Pyke 1984), limits on such movements can ultimately affect reproduction and population growth (Fryxell and Sinclair 1988; Middleton et al. 2018). Indeed, many studies have shown that behavioral responses to disturbances can influence individual performance (survival— McLoughlin et al. 2005; reproductive success—Dussault et al. 2012; Leclerc et al. 2014) and ultimately even macro-evolutionary patterns (speciation and adaptive radiation—Storch and Frynta 1999; Remes 2000; Morris 2003). Consequently, the studying the impacts of disturbances from a behavioral perspective is a relevant starting point to characterize, understand, and integrate the mechanisms underlying population and species resilience to disturbance.

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

Boreal forests provide excellent study systems for investigating the effects of meteorological conditions and anthropogenic disturbances on wildlife–habitat dynamics because weather is expected to vary more at higher latitudes in response to climate change (IPCC 2007). Boreal species have evolved adaptive strategies to accommodate long-term variation in the intensity and frequency of natural disturbances such as wildfires, windthrows, and insect outbreaks (Ostlund et al. 1997; McRae et al. 2001). Across the southern extent of the boreal forest, however, the rate of anthropogenic activity and resulting forest change now outpace that of natural disturbances as well as the resilience of affected communities (Vitousek et al. 1997; Sanderson et al. 2002; Cyr et al. 2009). Herbivore species can be particularly sensitive to habitat disturbances that may modify food availability and quality, as well as shelter (Stien et al. 2010; Leclerc et al. 2012a). Studying boreal herbivores can thus provide us with unique opportunities to investigate the mechanisms through which disturbances and weather affect ecological communities.

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

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

**Material and Methods**

**Study area.**—Our study area was located north of Lac Saint-Jean and the Saguenay River in Québec, Canada, and covers approximately 31,000 km² (Fig. 1), centered on Piraube Lake in the north (49°42′–51°00′N, 71°10′–72°09′W) and Portneuf Lake in the south (48°21′–49°45′N, 69°51′–71°12′W). The vegetation in the southern part of the study area was dominated by black spruce (Picea mariana) with balsam fir (Abies balsamea), white birch (Betula papyrifera), white spruce (Picea glauca), trembling aspen (Populus tremuloides), and jackpine (Pinus banksiana). The northern region of the study area was dominated by old-growth coniferous forest and open forest with black spruce, balsam fir, and jackpine stands. Mean annual temperatures range between −2.5°C and 0.0°C (extremes
ranging from −38°C to 33°C) and mean annual precipitation between 1,000 and 1,300 mm, of which 30–35% falls as snow (Robitaille and Saucier 1998). Moose (Alces americanus), gray wolves (Canis lupus), and black bears (Ursus americanus) are the other large mammal species found in the study area.

Industrial forestry is the main source of disturbance, with a logging history of ~50 years for the southern and ~25 years for the northern parts of the study area, resulting in ~59% and ~39% of their surface being under the influence of past fires, clearcuts, and forest roads when data were collected (Environment Canada 2012).

Caribou capture and telemetry survey.—We captured, radiocollared, and monitored 50 adult (>1.5 years of age at the time of capture) female caribou from 2004 to 2010 (13 to 24 per year for a total of 125 caribou-years, yielding 293,841 relocations) using global positioning system (GPS) collars (Lotek models 2 200L and 3 300L, and Telonics TGW-4680). Individuals were captured by net-gunning from a helicopter and recaptured periodically to retrieve data, change battery packs, or remove collars. Collars were also recovered following failure or death of an individual. Collars were programmed to acquire and record a GPS relocation at slightly different intervals (1–4 h). In addition, owing to occasional failure in position acquisition, the actual sampling interval also was not as regular as programmed, causing the mean sampling interval in our data set to be 2.3 ± 1.7 h (SD). Some individuals were tracked over several nonconsecutive periods, which were thus considered as distinct movement bouts in the subsequent analyses (see below for details), referred to as “tracks” (n = 70 tracks in total; Supplementary Data SD1). The cumulated time during which individual females were tracked ranged from ca. 6 weeks to ca. 5 years (see Supplementary Data SD1).

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

Our study followed American Society of Mammalogists guidelines (Sikes et al. 2016) and was carried out in strict accordance with the recommendations of the Canadian Council on Animal Care. Both captures and manipulations of study animals were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate #36-08-67). Captures were conducted on public lands, under the supervision of the Québec Government (i.e., Ministère des Forêts, de la Faune et des Parcs, hereafter MFFP), hence no specific permissions were required.
Habitat variables.—We used 1:20,000 digitized ecoforest maps published in 2000 by the MFFP to determine land-cover classes, and we updated these maps annually to include new habitat modifications resulting from forestry practices and natural disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for nonforested areas (e.g., water bodies). Based on studies conducted in the same system (Hins et al. 2009; Leclerc et al. 2012b, 2014; Beauchesne et al. 2013, 2014; Leblond et al. 2016a), we defined undisturbed habitat types as mature coniferous stands, while anthropogenic features consisted of clearcuts of varying age (0–5 and 6–20 years old) and roads. We did not include regenerating stands (20–40 years old) in our analyses due to multicollinearity. The effects of time since logging within each age category are considered minimal (Hins et al. 2009). We also characterized the topography of caribou habitat using elevation and terrain ruggedness. Terrain ruggedness was measured as the coefficient of variation of elevation (Leclerc et al. 2012b). We extracted habitat data for each GPS relocation using an 800-m radius buffer, based on results from preliminary first-passage time analyses on the entire study population (see below).

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

Residency time assessed using first-passage time.—We used a two-step approach based on first passage time (FPT) analysis (see Fauchald and Tveraa 2003 for more details, especially their figure 3) to estimate the time spent by an individual in an area (i.e., residency time). FPT is a measure of the time used by an individual to cross a circle of given radius (i.e., different radii refer to different scales) centered on each GPS relocation, and is thus related to residency time along each individual path. In a first exploratory step, we aimed at obtaining a general picture of the spatial scales at which individuals of our study population were using their habitat. We recalculated the positions along the tracks at 100-m intervals using the method provided by Calenge (2006; “rediscretizing”) and then calculated the variance of the natural log in FPT (\(\text{var}(\log(\text{FPT}))\)), following Fauchald and Tveraa (2003). FPT was calculated over a sequence of spatial scales with radii ranging from 100 to 15,000 m, using 100-m increasing intervals. Only tracks that covered more than 6 months of consecutive tracking (\(n = 51\) out of the 70 tracks) were used in this first step to avoid using tracks that would represent only a very short period of the annual cycle. The results were then averaged to investigate the occurrence of peaks in \(\text{var}(\log(\text{FPT}))\), indicative of spatial scales at which area-restricted search behavior takes place. We observed a peak in variance at radii of 800 m (Fig. 2) and this spatial scale was used in subsequent analysis.

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

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

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

### RESULTS

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

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

### Discussion

Most previous studies on movement and space-use patterns in terrestrial mammals investigated the effects of disturbed habitat types and linear features such as roads (e.g., Prokopenko et al. 2017; Monteith et al. 2018). Although some of those studies attempted to control for weather by dividing annual data into different biological periods (e.g., Leblond et al. 2010; van Beest et al. 2013), the effects of fine-scale variation in daily weather within a biological period have rarely been investigated (but see, e.g., Monteith et al. 2011; Middleton et al. 2013). Here, we showed that residency time (assessed using FPT) increased with colder weather and decreasing human disturbances. Those

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables included</th>
<th>No. of parameters (k)</th>
<th>General biological interpretation—Movement patterns are mostly affected by</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Intercept only</td>
<td>4</td>
<td>No fixed factors considered here (null model)</td>
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<tr>
<td>2</td>
<td>Precipitation + Temperature</td>
<td>6</td>
<td>Weather</td>
</tr>
<tr>
<td>3</td>
<td>Precipitation × Temperature</td>
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<td>Weather</td>
</tr>
<tr>
<td>4</td>
<td>Clearcut 0–5 + Clearcut 6–20 + Road density</td>
<td>7</td>
<td>Disturbance</td>
</tr>
<tr>
<td>5</td>
<td>Coniferous stands + Elevation + Ruggedness</td>
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<td>Habitat</td>
</tr>
<tr>
<td>6</td>
<td>Model 2 + Model 4</td>
<td>9</td>
<td>Weather + Disturbance</td>
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<tr>
<td>7</td>
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</tr>
<tr>
<td>8</td>
<td>Model 7 + Model 3</td>
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<td>Weather interacting with Disturbance</td>
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<td>10</td>
<td>Model 3 + Model 5</td>
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</tr>
<tr>
<td>11</td>
<td>Model 4 + Model 5</td>
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<td>Disturbance + Habitat</td>
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<td>13</td>
<td>Model 5 + Model 7</td>
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<td>14</td>
<td>Model 3 + Model 13</td>
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</tr>
</tbody>
</table>

*Defined as the coefficient of variation of elevation.*
relationships, however, did not hold in all biological periods. Disturbances had a larger effect on residency time than daily weather during calving and summer, but this was reversed during winter and spring. Therefore, our results only partially supported our prediction that daily weather would have a weaker effect than habitat disturbances on residency time. Our results highlight the importance of studying animal behavior over complete annual cycles as the effects of weather and disturbances on the movement may vary seasonally. Finally, we found no evidence that residency time in disturbed habitats was modulated by daily weather in our study system.

Herbivore movement behavior serves several purposes, including finding food resources, avoiding predators, and finding shelter (Dussault et al. 2004; Leclerc et al. 2012b; Merkle et al. 2016). Our results suggest that movements of caribou likely aim to reduce predation risk. By increasing residency time in mature coniferous stands, at higher elevation, and in rugged terrain, caribou can decrease the rate of encounters with predators such as wolves which usually use lower elevations and flat terrain (Whittington et al. 2011; Lesmerises et al. 2012). Also, caribou tend to reduce residency time with increasing road density. The presence of roads is associated with higher encounter rate and predation risk by wolves (James and Stuart-Smith 2000; Whittington et al. 2011), and roadsides are highly productive environments that are also selected by other predators of caribou such as black bears, particularly during the onset of bud growth in spring and summer (Bastille-Rousseau et al. 2011). Avoidance of human disturbances, especially roads, during calving has been shown for boreal caribou in Québec (Leclerc et al. 2012b). Avoidance of disturbed habitat by females with calves is known to increase their reproductive success (Leclerc et al. 2014) and likely have impacts at the population level because calf survival can greatly influence population dynamics (Gaillard et al. 2000). Our results are in line with previous work on boreal caribou that suggests that the current recession of the southern limit of this threatened species is linked to anthropogenic disturbances (Schaefer 2003; Vors et al. 2007; Festa-Bianchet et al. 2011) via maladaptive behavioral responses (Leclerc et al. 2014; Losier et al. 2015; Lafontaine et al. 2017). Anthropogenic disturbances reduce the area of their prime habitat and trigger the numerical and functional responses of alternative prey and predators (Seip 1992; Wittmer et al. 2005; Courtois et al. 2008; DeCesare et al., 2010). Reduction of residency time in disturbed landscape and in areas with higher predation risk was also observed in elk (Cervus elaphus). Indeed, elk reduce their rate of movement and increase their residency time when hunter access (mainly roads) is limited and when the occurrence of predators is lower (Prair et al. 2005; Cleveland 2012).

Table 2.—Difference in AIC (ΔAIC) from the top-ranked model (bold), AIC weight (ω), 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 descriptions. Models with ΔAIC < 2 were considered competitive and are shown in italics.

<table>
<thead>
<tr>
<th>Model</th>
<th>Winter</th>
<th>Spring</th>
<th>Calving</th>
<th>Summer</th>
<th>Rut</th>
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<tr>
<td></td>
<td>ΔAIC</td>
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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.

<table>
<thead>
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<th>Variable</th>
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<td>Intercept</td>
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</tr>
<tr>
<td>Coniferous</td>
<td>0.232</td>
<td>0.204</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.116</td>
<td>0.058</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>0.016</td>
<td>−0.011</td>
</tr>
<tr>
<td>Precipitation x Temperature</td>
<td>0.013</td>
<td>−0.005</td>
</tr>
</tbody>
</table>
The strongest negative effect of road density and the strongest positive effects of elevation and terrain ruggedness were observed during calving and summer: both variables are associated with an increased avoidance of predation risk. Calving and summer are the most critical periods for female reproductive success as the calves are highly vulnerable to predation (Pinard et al. 2012; Leclerc et al. 2014). In addition, all females showed similar behavioral responses to natural habitat types and human disturbances during calving, as shown by the very low variance explained by random effects (Supplementary SD3). We consider that natural selection may have shaped such behavioral responses during this critical phase. In contrast, the higher individual variation in movement behavior measured during other biological periods could indicate that appropriate responses to human disturbances and adverse weather conditions can be achieved through different tactics that maintain phenotypic variation. However, further studies will be necessary to confirm this hypothesis, and would for instance involve measurements of indices of individual state (e.g., body mass and stress hormone levels) and fitness (e.g., calf survival).

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

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

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

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

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**Supplementary Data**

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

**Supplementary Data SD1.**—Summary of the GPS tracking of 50 adult female caribou (*Rangifer tarandus caribou*). Some individuals were tracked for several nonconsecutive 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).

**Supplementary Data SD2.**—Distribution of values for each variable in the data set used to determine residency time of adult female caribou (*Rangifer tarandus caribou*), based on first-passage time analyses conducted within 800-m radius circles centered on all successive GPS relocations. Please note that the distribution shows the raw values, 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 calculated using first-passage time analyses conducted within 800-m radius circles centered on all successive GPS relocations, for each biological period.

**Supplementary Data SD4.**—Relative importance of each variable for each biological period in explaining residency time (assessed using first-passage time analyses conducted within 800-m radius circles centered on all successive GPS relocations) 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).

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