

# Predicting how climate change will affect how and where terrestrial mammals will move in British Columbia, Canada

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## **Abstract**

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move, with cascading effects on individuals' fitness and habitat selection at the population, community, and ecosystem levels. Previous research has quantified the effects of temperature on mammalian movement behaviour, but few have quantified the effects of future climate change on fine-scale movement and habitat selection. We address this gap by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on mammals' movement rates and habitat selection. We then leverage the estimated effects to predict how and where mammals will move in British Columbia (BC), Canada, throughout the 21<sup>st</sup> century. We show that changes in temperature altered movement phenology, and that climate change will impact mammals' movement rates and habitat selection throughout the century, but that there are no common trends across all study species. Consequently, we suggest that species' responses be interpreted carefully and considered jointly when extrapolating the community-level consequences of climate change.

## <sup>1</sup> 1 Introduction

<sup>2</sup> For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan  
<sup>3</sup> *et al.*, 2008). Animals move to maximize resource availability (e.g., food, water, shelter, see:  
<sup>4</sup> Charnov, 1976; Kacelnik, Krebs & Bernstein, 1992), optimize habitat use (Winter *et al.*,  
<sup>5</sup> 2024), and escape predation (Peterson, Soto & McHenry, 2021; Tan *et al.*, 2024; Bartashevich  
<sup>6</sup> *et al.*, 2024). However, ambient temperature affects mammals' movement rates by altering  
<sup>7</sup> the energetic cost of movement (Taylor, Heglund & Maloij, 1982; Brown *et al.*, 2004; Fuller *et*  
<sup>8</sup> *al.*, 2016; Jahn & Seebacher, 2022), the ease of movement (e.g., snow depth and density, see  
<sup>9</sup> Montgomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and the risk of overheating  
<sup>10</sup> (Heten *et al.*, 2014; Dyer *et al.*, 2023). Additionally, temperature also affects movement  
<sup>11</sup> indirectly by through other drivers of movement behaviour, such as trophic interactions  
<sup>12</sup> (Hegel *et al.*, 2010) and the value of resources (e.g., water, heat, shelter – see: Elmore *et*  
<sup>13</sup> *al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019). Changes in temperature thus  
<sup>14</sup> affects how animals move (e.g., movement frequency and speed – their movement behaviour:  
<sup>15</sup> Nathan *et al.*, 2008; Dyer *et al.*, 2023) and where they move to (i.e., their habitat selection:  
<sup>16</sup> Merkle *et al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*, 2023).

<sup>17</sup> Temperature also affects the consequences of animal movement, such as encounter rates  
<sup>18</sup> with resources (Mezzini *et al.*, 2025), other animals (Martinez-Garcia *et al.*, 2020), and  
<sup>19</sup> humans (Weststrate *et al.*, 2024), and these changes are exacerbated at extreme temperatures  
<sup>20</sup> (Wilson *et al.*, 2001; Berger *et al.*, 2018; Giroux *et al.*, 2023). But what counts as “extreme”  
<sup>21</sup> varies across species: thermal specialists are more sensitive to small changes outside their  
<sup>22</sup> typical range (e.g., Giroux *et al.*, 2023), while thermal generalists can adapt more easily  
<sup>23</sup> to change (Dupont *et al.*, 2024). However, generalists' greater adaptability is tested when  
<sup>24</sup> they are subject to changes that are more severe (McCain, 2019), affect many factors (e.g.,  
<sup>25</sup> temperature, phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to  
<sup>26</sup> respond within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016;

<sup>27</sup> Xu *et al.*, 2021).

<sup>28</sup> In the last 200 years, many ecosystems experienced widespread warming that resulted  
<sup>29</sup> in milder and shorter winters, hotter and longer summers, and a greater risk of extremely  
<sup>30</sup> high temperatures and severe forest fires (Zurowski, 2023; IPCC, 2023). Over the next  
<sup>31</sup> 100 years, these changes are expected to worsen and continue to impact mammals' fitness,  
<sup>32</sup> movement behaviour, and habitat selection as animals cope with growing heat stress (Deb,  
<sup>33</sup> Forbes & MacLean, 2020; Woo-Durand *et al.*, 2020) and more frequent and intense extreme  
<sup>34</sup> events (Bunnell, Kremsater & Wells, 2011), along with increasing anthropogenic pressure  
<sup>35</sup> (Sawyer *et al.*, 2009; Sih, Ferrari & Harris, 2011; Weststrate *et al.*, 2024). Consequently,  
<sup>36</sup> it remains unclear how or whether species will be able to respond to climate change in the  
<sup>37</sup> current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially  
<sup>38</sup> when populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or  
<sup>39</sup> are physiologically incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018).  
<sup>40</sup> Uncertainty in future conditions and their consequences on ecosystems present a need for a  
<sup>41</sup> comprehensive understanding of (1) the direct effects of temperature on animal movement  
<sup>42</sup> behaviour and (2) the implications this will have on populations and species' adaptability  
<sup>43</sup> and resiliency, community structure, and biodiversity at large. Recent work has documented  
<sup>44</sup> the effects of climate change on mammals' ranges (Leclerc *et al.*, 2021), movement behaviour  
<sup>45</sup> (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses  
<sup>46</sup> (McCain, 2019), but it is still unclear how mammals will adapt their small-scale movement  
<sup>47</sup> and habitat selection to changes in temperature during the 21<sup>st</sup> century (IPCC, 2023; but  
<sup>48</sup> see Hetem *et al.*, 2014; Winter *et al.*, 2024).

<sup>49</sup> Understanding the direct and indirect impacts of temperature on mammalian movement  
<sup>50</sup> is essential for decision makers to be able to prepare for and respond to change in a proac-  
<sup>51</sup> tive manner (e.g., Sawyer *et al.*, 2009; McCain, 2019). The Canadian province of British  
<sup>52</sup> Columbia is currently experiencing rapid widespread warming (Turner & Clifton, 2009; Dier-  
<sup>53</sup> auer, Allen & Whitfield, 2021), phenological shifts (Basu *et al.*, 2024; e.g., Tysor, 2025), and

more frequent and intense extreme events (e.g., Zhang *et al.*, 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands and oceans by 2030 (Section H, Targets 2 and 3 of Convention on Biological Diversity, 2022), decision makers must understand which areas will be of greatest value for maximizing the project’s effectiveness. Predicting how climate change will affect how, when, and where animals will move is necessary for identifying which landscapes are most valuable now as well as in the future. Failing to understand how changes in temperature will affect mammalian movement behaviour and habitat selection will hinder our ability to respond to the current climate crisis and make decisions that are viable in the long term.

This paper provides an analysis of the effects of air temperature on the movement of six terrestrial mammal species in British Columbia (BC), Canada (*Canis lupus*, *Cervus canadensis*, *Oreamnos americanus*, *Puma concolor*, boreal and southern mountain *Rangifer tarandus*, and *Ursus arctos horribilis*; Table 1). Using over 25 years of telemetry data throughout a large spatial range of British Columbia and hourly air temperature data, we estimate how mammals altered their probability of movement, speed when moving, and habitat selection in response to temperature. We then pair the estimated responses with climate change projections to forecast the species’ movement during the 21<sup>st</sup> century under different climate-change scenarios (referred to as Shared Socioeconomic Pathways, SSPs – see Riahi *et al.*, 2017). We disentangle the direct and indirect effects of temperature on the movement behaviour of terrestrial mammals and discuss the consequences of these changes at the individual, population, and landscape levels.

Table 1: Start and end of the GPS telemtries along with the median sampling interval ( $\Delta t$ ; stratified by individual), number of animals (Animals), and number of animals with resolved speed (Has speed) for each of the species in this study.

Species	Start	End	$\Delta t$ (hours)	Animals	Has speed
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25	39	39

Species	Start	End	$\Delta t$ (hours)	Animals	Has speed
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00	169	169
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.25	11	10
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	29	29
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	13.00	146	131
<i>Rangifer tarandus</i> (s. mountain)	1998-03-21	2009-06-07	6.00	22	20
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	18

## 76 2 Methods

### 77 2.1 Datasets used

78 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry  
 79 data (Fig. 1); (2) historical hourly reanalyzed air temperature from the ERA5 dataset from  
 80 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent  
 81 forest cover, elevation, and distance from water; and (4) climate change projections under  
 82 four Shared Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). We detail the data  
 83 sources and analyses in the sections below.

#### 84 2.1.1 GPS telemetry data

85 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
 86 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou  
 87 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public BC Oil and  
 88 Gas Research and Innovation Society repository ([https://www.bcgis.ca/projects/boreal-](https://www.bcgis.ca/projects/boreal-caribou-telemetry-data)  
 89 **MISSING INFO ON OTHER TELEMETRY DATA**  
 90 Clearly erroneous GPS locations were removed using diagnostic plots of (1) distance from  
 91 the median location, (2) straight-line displacement between locations, (3) turning angle,  
 92 and (4) time interval between consecutive points. Particular attention was paid to points

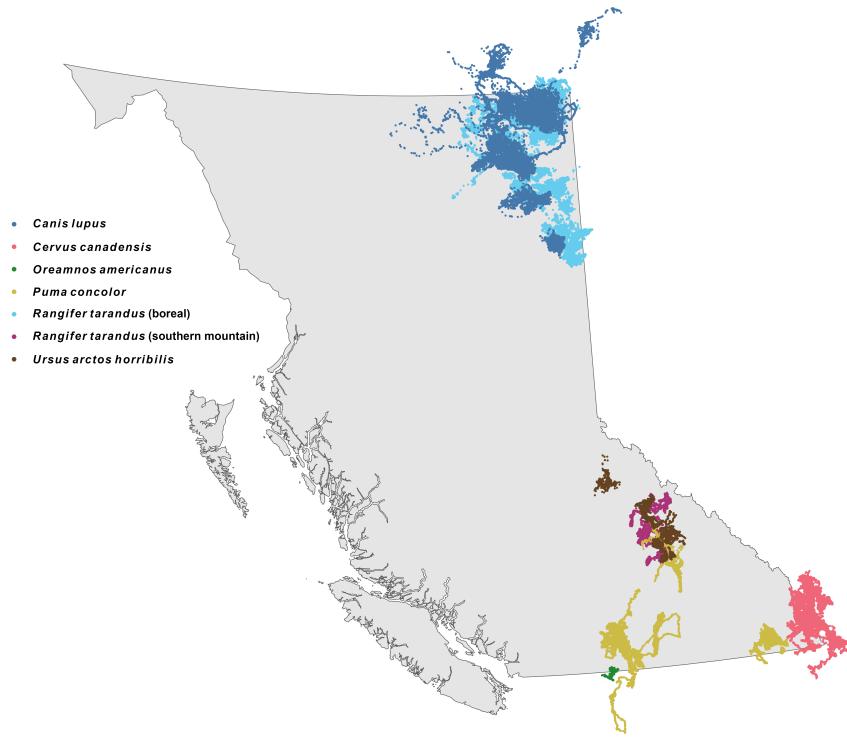


Figure 1: GPS telemetry data for the six species in this study.

93 with large turning angles ( $\gtrsim 170^\circ$ ) and excessively high straight-line displacement, es-  
 94 pecially if antecedent and subsequent points indicated stationary behaviour. The script  
 95 used to clean the data and all associated custom functions are available on GitHub at  
 96 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

### 97 2.1.2 Historical and projected temperature data

98 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset  
 99 (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting  
 100 server (ECMWF; [www.ecmwf.int](http://www.ecmwf.int); <https://cds.climate.copernicus.eu>). Proximal tempera-  
 101 ture was estimated for each location by extracting the value from the corresponding raster  
 102 cell from the temporally nearest raster using the `extract()` function from the `terra` package  
 103 (version 1.7-46, Hijmans, 2023) for R (R Core Team, 2024).

104 We obtained rasters of projected monthly average temperature at a  $0.08^\circ$  resolution in BC  
 105 from 2020 to 2100 under the different SSPs via the `climatenar` package (version 1.0, Burnett,

106 2023) for R. Since the climate projections only provided monthly means and ranges but no  
107 measures of variance or distributional assumptions, we used the hourly ERA5 data for BC  
108 from 1998 to 2023 (extremes included, see Hersbach *et al.*, 2023) to calculate within-month  
109 variance in temperature, which we defined as the variance within a given pixel, month, and  
110 year. We then modeled the estimated variance using a GAM for location and scale (GAMLS,  
111 see: Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017).  
112 The linear predictor for the location (i.e., the mean) included smooth terms of the within-  
113 pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-  
114 dimensional smooth of space, and a tensor interaction product term of space and month. The  
115 linear predictor for the scale term (which governs the mean-variance relationship) included  
116 smooth terms of the monthly mean, month, and space. We did not include a smooth of year  
117 to avoid unrealistic projections when extrapolating beyond the range of historical data.

118 We simulated hourly variation in future weather by assuming hourly temperature followed  
119 a normal distribution with mean specified by the monthly `climatenetR` climate projections  
120 and variance as specified by the Gamma GAMLS. We then predicted changes in movement  
121 behaviour and habitat selection as a function of the simulated temperature using the HGAMs  
122 and HRSFs. For each month within each year from 2020 to 2100, we simulated hourly  
123 weather by including temperatures from the 0.1 to the 0.9 quantile by increments of 0.1, and  
124 we weighted each quantile proportionally to the (normalized) Gaussian probability density  
125 for each quantile.

### 126 2.1.3 Resource rasters

127 We estimated percent forest cover and distance from water using the rasters created by  
128 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
129 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
130 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
131 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover

132 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the  
133 nearest pixel with water using the `distance()` function from the `terra` package. Finally,  
134 we obtained two digital elevation models using the `get_elev_raster()` function from the  
135 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom  
136 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate  
137 change projections via `climatenar`. All final rasters and code are available on GitHub at  
138 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

139 **2.2 Estimating mammals' instantaneous speeds**

140 We modeled each animal's movement using continuous-time movement models (Fleming *et*  
141 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then  
142 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all  
143 models with finite speed estimates (415 of 433, see Fleming *et al.*, 2014; Noonan *et al.*,  
144 2019a). The 18 animals with insufficiently fine sampling were for one mountain goat, 15  
145 boreal caribou, and 2 southern mountain caribou (Table 1).

146 Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-  
147 gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
148 minimum instantaneous speed could be 0. We performed this correction by subtracting  
149 each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
150 used is available on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals->  
151 [temperature/blob/main/functions/detrend\\_speeds.R](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively  
152 small, non-zero speeds, we determined whether an animal was moving or not using the in-  
153 flection point of each species' histogram of detrended speed estimates, as  $k$ -nearest neighbors  
154 did not discriminate between states well (Fig. S3).

155 **2.3 Estimating the effects of temperature on mammals' movement**

156 The following sections detail the statistical framework and modelling we used to estimate  
157 the effect on temperature on mammals' movement. To assess the importance of including  
158 temperature as an explicit covariate (rather than including its effects with time of day and  
159 day of year), we fit models with and without smooth effects of temperature and compared  
160 the deviance explained, model predictions, and AIC values of the two sets of models.

161 **2.3.1 Effects of temperature on movement rates**

162 We estimated the effects of temperature ( $^{\circ}\text{C}$ ) on mammals' movement state (moving or  
163 not) and speed when moving using two Hierarchical Generalized Additive Models (HGAMs,  
164 see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version  
165 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was mov-  
166 ing,  $P(M)$ , with a binomial family of distributions and logit link function. The response  
167 variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an  
168 animal's speed when moving (`speed`) with a gamma family of distributions and log link func-  
169 tion. The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`),  
170 fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(..., by`  
171 `= species`)`), which allowed each species' term to be estimated independent of other species  
172 (see model I in Figure 4 of Pedersen et al., 2019). The by smooths accounted for trends  
173 in time of day (in Pacific Daylight Time; tod_pdt), day of year (doy), and temperature  
174 (temp_c). Additionally, the models had three tensor product interaction terms (ti()) by  
175 each species: (1) day of year and time of day, (2) temperature and time of day, and (3)  
176 temperature and day of year. These three terms accounted for: (1) seasonal changes in day  
177 length, (2) hourly changes in the response to temperature (e.g., changes in nocturnality),  
178 and (3) seasonal changes in the response to temperature (e.g., changes in coats and migra-  
179 tion timing). Finally, smooth terms of log-transformed hours between GPS locations (dt)  
180 accounted for irregular sampling rates. A global term of log(dt) accounted for the overall`

181 effect of sampling interval, while a factor-smooth interaction term (`s(log(dt), species,`  
182 `bs = 'fs')`) allowed for species-level deviations from the global term while assuming a com-  
183 mon smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).  
184 The HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic  
185 splines (`bs = 'cc'`; see p. 202 of Wood, 2017). Together, the binomial HGAM and the  
186 gamma HGAM inform us on an animal's long-term average speed, since it is the product of  
187 the probability of moving and its average speed when moving. We fit the models with fast  
188 REML ('`fREML`') and discretized covariates (`discrete = TRUE`) to optimize computational  
189 efficiency with no appreciable losses to model performance (Wood, Goude & Shaw, 2015;  
190 Wood *et al.*, 2017; Li & Wood, 2020). Additional details are provided in Appendix A.

```

m_moving <- bam(
  moving ~
    s(animal, bs = 're') +
    species + #' necessary since `by` terms do not include intercept terms
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  data = d,
  method = 'fREML', # fast REML
  discrete = TRUE, # discretize the covariates for faster computation
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5))) #' for `bs = 'cc'` 

m_speed <- bam(
  speed_est ~
    s(animal, bs = 're') +
    species +
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  family = Gamma(link = 'log'),
  data = d_2, #' data filtered for only moving
  method = 'fREML',
  discrete = TRUE,
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5)))

```

### 191 2.3.2 Effects of temperature on habitat selection

192 We estimated the effects of temperature on each species' selection for percent forest cover  
 193 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 194 ting a Hierarchical Resource Selection Function for each species using an HGAM with a Pois-  
 195 son family of distributions and log link function (Appendix B, also see Aarts *et al.*, 2008).  
 196 We accounted for the spatiotemporal autocorrelation in the telemetry locations by weighting  
 197 each point based on the telemetry's Autocorrelated Kernel Density Estimate (Fleming &  
 198 Calabrese, 2017; Noonan *et al.*, 2019b) to produce estimates of second- and third-order habi-  
 199 tat selection (*sensu* Johnson, 1980). While we recognize there are other important drivers  
 200 of habitat selection (e.g., forest age, forest type, prey availability), we decided to only use  
 201 these three proxies to produce results that are comparable between species and to make  
 202 province-wide predictions simpler. Each species' model had the same structure:

```

rsf <- bam(
  detected ~ # 1 for telemetry locations, 0 for quadrature points
  # species-level average resource preference
  s(forest_perc, k = 6, bs = 'tp') +
  s(elevation_m, k = elev_k, bs = 'tp') +
  s(dist_water_m, k = 6, bs = 'tp') +
  # animal-level deviations from the species-level average
  s(animal, bs = 're') +
  s(forest_perc, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(elevation_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(dist_water_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  # changes in preference with temperature
  ti(forest_perc, temp_c, k = 6, bs = 'tp') +
  ti(elevation_m, temp_c, k = 6, bs = 'tp') +
  ti(dist_water_m, temp_c, k = 6, bs = 'tp') +
  # include marginals of temperature to remove sampling biases
  s(temp_c, k = 4, bs = 'tp') +
  s(temp_c, animal, k = 4, bs = 'fs', xt = list(bc = 'cr')),
  family = poisson(link = 'log'),
  data = d, # species-specific dataset
  weights = weight, # based on AKDE
  method = 'fREML',
  discrete = TRUE)

```

203     Smooth effects of percent forest cover, elevation, and distance to water accounted for  
 204     the species-level average selection strength for each resource. A random effect for each in-  
 205     dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
 206     while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
 207     selection (i.e., individual-level deviations from the species-level average). Tensor interaction  
 208     product terms (`ti()`) of the three resources and temperature estimated the change in re-  
 209     source selection at different temperatures. Finally, we included marginal smooth terms of  
 210     temperature to account for species- and individual-level sampling biases over temperature  
 211     (e.g., sampling more during warm periods). Detections were weighted proportionally to their  
 212     degree of independence from other temporally proximate detections (`weights = weight` –  
 213     see Appendix B and Alston *et al.*, 2022), while quadrature points had a weight of 1. Quadra-  
 214     ture points were obtained using all raster cells in the 99.9% AKDE percentile. The number  
 215     of quadrature locations greatly outnumbered the number of observed locations (Fig. S13),  
 216     especially after accounting for weighting based on the degree of autocorrelation and the  
 217     number of home range crossings (Fig. S14).

<sup>218</sup> **3 Results**

<sup>219</sup> Data were relatively scarce for temperatures lower than  $-20^{\circ}\text{C}$  or above  $20^{\circ}\text{C}$  (Fig. S4).  
<sup>220</sup> Species differed in overall mean probabilities of movement (range: 0.05 – 0.3), mean speed  
<sup>221</sup> when moving (range: 0.42 – 2.7 km/day), and mean distance traveled (range: 0.04 – 0.6  
<sup>222</sup> km/day; Table 2). Grizzly bears tended to move least often (probability of moving  $P(M) \approx$   
<sup>223</sup> 0.05), while wolves and pumas moved most often ( $P(M) \gtrapprox 0.23$ ). When moving, mountain  
<sup>224</sup> goats and southern mountain caribou moved the slowest ( $\mathbb{E}(S|M) \approx 0.4 \text{ m/s}$ ), while wolves  
<sup>225</sup> had the highest mean speed when moving ( $\mathbb{E}(S|M) \approx 2.7 \text{ m/s}$ ). Consequently, wolves  
<sup>226</sup> traveled, on average, 50 km/day – 2.5 to 16.7 times further than other mammals.

Table 2: Mean probability of movement ( $P(M)$ ), speed when moving ( $\mathbb{E}(S)$ , m/s), and distance travelled ( $\mathbb{E}(D)$ , m/s) as estimated by models without and with temperature ( $\mathbb{E}(\dots|T)$ ), after post-stratification to a 1-hour sampling rate and a temperature of  $T = 0^{\circ}\text{C}$ .

Species	$\hat{P}(M)$	$\hat{P}(M T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>C. canadensis</i>	0.16	0.17	0.57	0.57	0.09	0.10
<i>Canis lupus</i>	0.23	0.22	2.64	2.67	0.61	0.60
<i>O. americanus</i>	0.15	0.13	0.43	0.42	0.06	0.06
<i>Puma concolor</i>	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus</i> (SM)	0.11	0.11	0.43	0.42	0.05	0.05
<i>R. tarandus</i> (boreal)	0.19	0.18	0.71	0.73	0.14	0.13
<i>U. arctos horr.</i>	0.05	0.05	0.72	0.72	0.04	0.04

<sup>227</sup> Near  $0^{\circ}\text{C}$ , wolves preferred dense forest cover ( $\gtrapprox 50\%$ ) high elevations, and distances  
<sup>228</sup> from water  $< 10 \text{ km}$ ; elk preferred intermediate forest cover, elevations between 1 and 2 km,  
<sup>229</sup> and distances from water of 5-15 km; mountain goats preferred sparse ( $< 50\%$ ) forest cover,  
<sup>230</sup> elevations between 1 and 2 km; pumas preferred high forest cover, an elevation of  $\sim 1 \text{ km}$ ,  
<sup>231</sup> and distances from water  $< 10 \text{ km}$ ; boreal caribou selected for intermediate to high forest  
<sup>232</sup> cover, elevations near 500 m, and distances from water  $< 10 \text{ km}$ ; southern mountain caribou  
<sup>233</sup> selected for dense forest cover, elevations near 2 km, and distances from water  $< 5 \text{ km}$ ; and  
<sup>234</sup> grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances

<sup>235</sup> from water < 2 km.

<sup>236</sup> Including temperature in the models always increased within-sample prediction, but  
<sup>237</sup> the change was not always substantial (deviance explained increased between +0.2% and  
<sup>238</sup> +18.6%, with all HRSFs having an increase  $\geq +4.6\%$ ), and there was relatively strong  
<sup>239</sup> agreement between models with and without temperature (Figs. S5 and S13), but including  
<sup>240</sup> temperature resulted in substantially lower AIC values for all models, especially HRSFs (all  
<sup>241</sup>  $\Delta\text{AIC} \leq -342$ ; Table 3). Although this may be interpreted as better fit, it is important to  
<sup>242</sup> note that AIC generally decreases with more complex terms when sample sizes are large,  
<sup>243</sup> even if the more complex model is not closer to the true model (see section 1.8.6, pages 52-54  
<sup>244</sup> of Wood, 2017).

Table 3: Changes in deviance explained ( $\Delta\text{DE}$ ) and Akaike Information Criterion ( $\Delta\text{AIC}$ ) from including temperature in the models estimating probability of movement ( $P(\text{moving})$ ) and speed when moving (Speed) as well as in species-level Hierarchical Resource Selection Functions (HRSF).

Model	Species	$\Delta\text{DE}$	$\Delta\text{AIC}$
$P(M)$	All	0.5%	-5927
Speed	All	0.2%	-1682
HRSF	<i>Canis lupus</i>	9.2%	-6566
HRSF	<i>Cervus canadensis</i>	4.6%	-4448
HRSF	<i>Oreamnos americanus</i>	18.6%	-813
HRSF	<i>Puma concolor</i>	8%	-966
HRSF	<i>Rangifer tarandus</i> (boreal)	5.3%	-5637
HRSF	<i>Rangifer tarandus</i> (s. mountain)	12%	-342
HRSF	<i>Ursus arctos horribilis</i>	17.7%	-914

245 **3.1 Effects of temperature on movement rates**

246 The effects of temperature on movement rates varied in both direction and magnitude across  
 247 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
 248 migration, hibernation; see Figs. S6-S8). Smooth interaction terms were well-behaved and  
 249 indicated clear shifts in activity over time of day and day of year for all species. The models  
 250 explained reasonably high proportions of the deviance (10.7% for the binomial model and  
 251 79.3% for the Gamma model) and had good in-sample prediction (Fig. S9). All species  
 252 adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 2).  
 253 For example, wolves, elk, pumas, and boreal caribou reduced their mid-day and summer  
 254 movement rates when temperatures were above 20°C. However, uncertainties around the  
 255 estimated effects were often higher at extreme temperatures due to data scarcity. All species'  
 256 estimated probability of moving decreased with sampling intervals approximately above 1  
 257 hour, and most species' estimated speed when moving decreased monotonically with sampling  
 258 interval, although the estimated trends were highly uncertain for some species (Fig. S10).

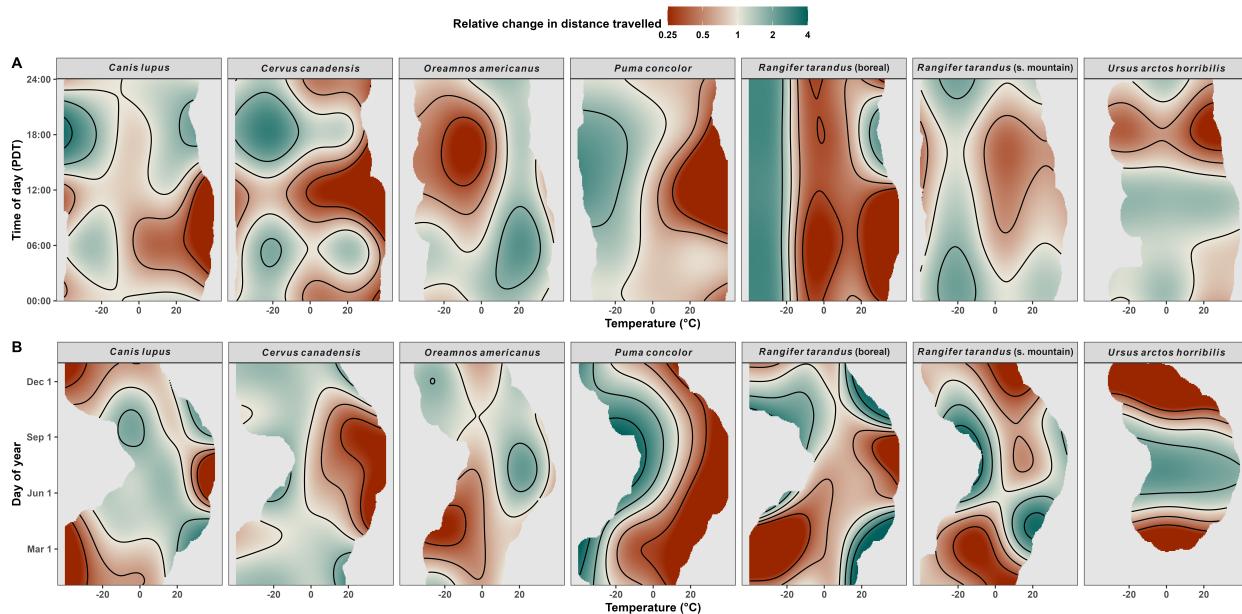


Figure 2: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year at 12:00 PDT (**B**). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the log<sub>2</sub> scale to help visualize patterns in doubling, and values are capped to -75% and +300% (i.e., 2<sup>±2</sup>) for ease of readability.

259 **3.2 Effects of temperature on habitat selection**

260 Species' relative selection strength (RSS) was generally strongest for elevation and weak-  
 261 est for forest cover, but species' RSS for resources depended on temperature. Changes in  
 262 RSS with temperature were also strongest for elevation and generally weakest distance from  
 263 water, but there were no common trends across all species for any of the three resources.  
 264 All species, with the exception of pumas, exhibited a clear temperature-dependent shift  
 265 in their preference for forest cover. At higher temperatures, wolves, mountain goats, and  
 266 grizzly bears became less selective for forest cover, while elk and caribou shifted towards  
 267 more intermediate forest cover without much of a change in preference width. All species  
 268 shifted elevationally with temperature, although boreal caribou did not exhibit as strong  
 269 of a change. As temperatures rose, elk, mountain goats, and pumas increased in elevation,  
 270 while boreal wolves, southern mountain caribou, and grizzly bears decreased in elevation.  
 271 Most species generally remained within 5 km of water, and temperature did not affect their  
 272 selection strength as much as for the other two resources. Again, estimated RSS values were  
 273 generally most uncertain at extreme temperatures (Fig. S13).

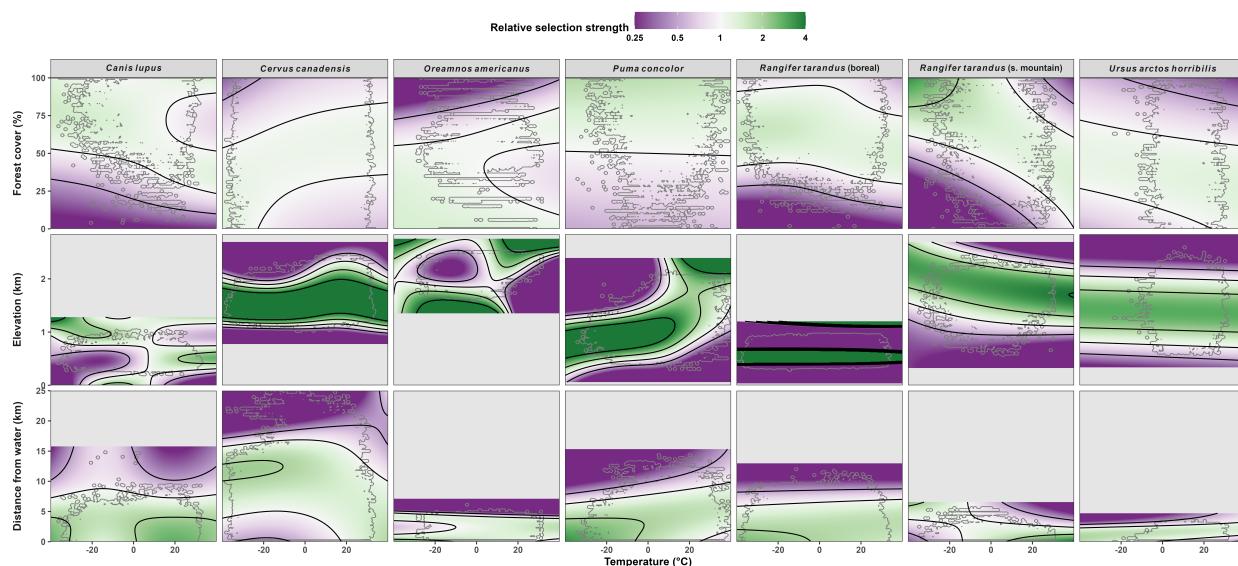


Figure 3: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were re-centered and capped to  $2^{\pm 2}$  to improve readability.

<sup>274</sup> **3.3 Predicted changes in movement during the 21<sup>st</sup> century**

<sup>275</sup> Species varied in both the direction and magnitude of predicted change in distance traveled,  
<sup>276</sup> but worse climate-change scenarios always corresponded to greater absolute changes in be-  
<sup>277</sup> haviour (Figs. 4, S11, and S12). Under the best-case scenario, absolute changes by 2100  
<sup>278</sup> were small (approximately 0% to 4%), while under the worst-case scenario absolute changes  
<sup>279</sup> ranged from ~2% (grizzly bear) to ~25% (pumas), although the models did not explicitly  
<sup>280</sup> account for changes in hibernation phenology. Throughout BC (Fig. 5), all species showed  
<sup>281</sup> little to no absolute change under the best-case scenario (approximately 0-4% relative to  
<sup>282</sup> 2025, on average), and approximately 2-25% average absolute change under the worst-case  
<sup>283</sup> scenario, but the predicted changes varied spatially due to heterogeneity in climate change.  
<sup>284</sup> Again, absolute changes were smallest under the best-case scenario and greatest under the  
<sup>285</sup> worst-case scenario for all species.

<sup>286</sup> All species exhibited a decrease in RSS within their current range, irrespective of climate  
<sup>287</sup> change scenario. Changes were often were only between -1% and -3% under the best-case  
<sup>288</sup> scenario but they ranged from -8% to -14% under the worst-case scenario (6). As with  
<sup>289</sup> distance traveled, the change in RSS in 2100 varied throughout BC for all species (Fig. 7).  
<sup>290</sup> All species were predicted to exhibit a decrease in RSS throughout most of BC, with the  
<sup>291</sup> exception of boreal caribou, which had a predicted increase in approximately 67% of the  
<sup>292</sup> province, including their current range. The increase was in great part due to the estimated  
<sup>293</sup> increase in selection for high-elevation areas that are well outside the population's current  
<sup>294</sup> range.

<sup>295</sup> **4 Discussion**

<sup>296</sup> We have demonstrated that temperature is an important determinant of whether, how,  
<sup>297</sup> and where mammals move, even while accounting for seasonality (e.g, changes in photope-  
<sup>298</sup> riod, hormones, and resources). Disentangling temperature from other drivers allowed us

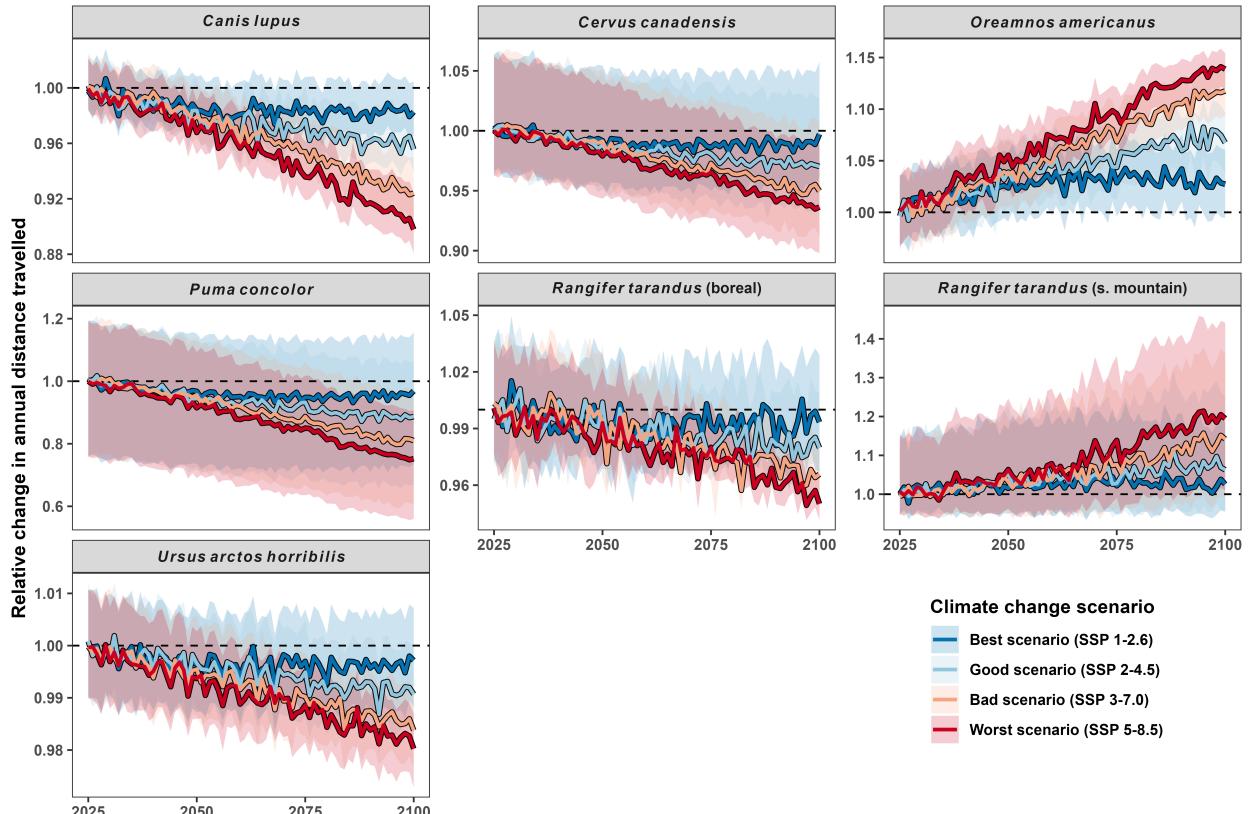
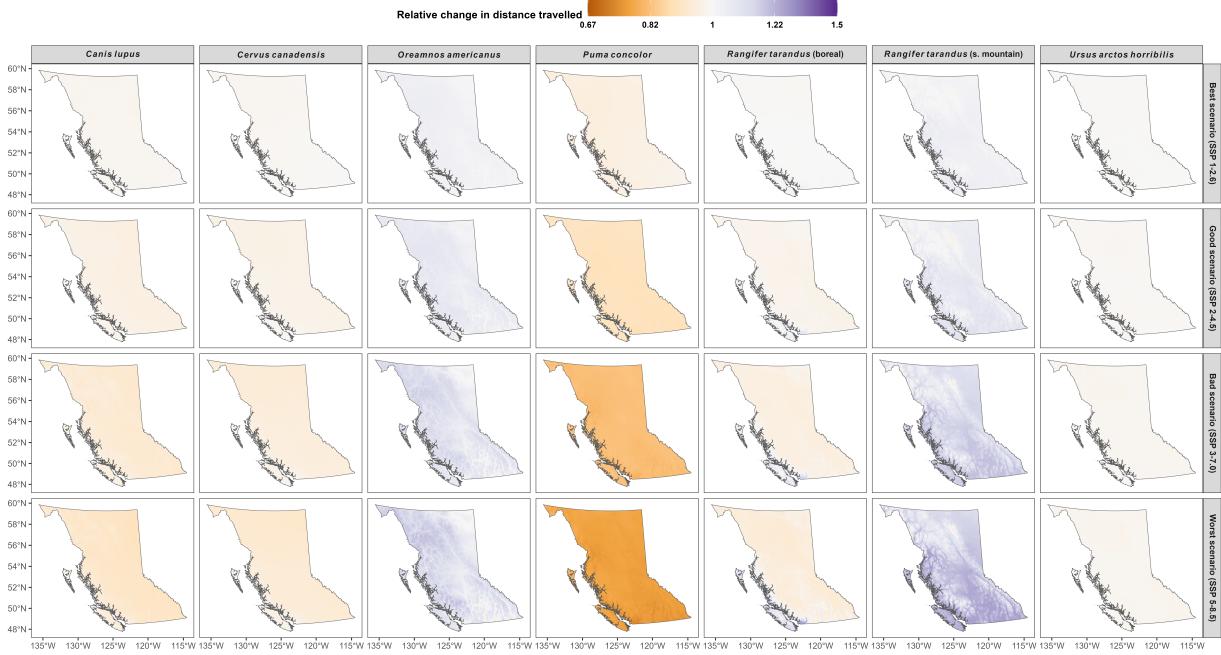


Figure 4: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the 90% prediction interval within the range. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.



**Figure 5: Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values  $< 1$  indicate a decrease, and values  $> 1$  indicate an increase. For ease of readability, the color bar is on the  $\log_2$  scale to help visualize patterns in doubling, and values are capped to 0.8 and 1.25 ( $\approx 2^{\pm 0.58}$ ; original data ranged 0.72 to 1.29). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest cover.

299 to predict how changes in climate will affect mammalian movement even if all other drivers  
 300 remain approximately constant or adapt at negligible rates. However, predicting mammals'  
 301 responses to climate change becomes increasingly complex as habitats warm and animals  
 302 are exposed to increasingly frequent conditions that are both extreme and novel. Predicting  
 303 mammals' responses at the data-scarce fringes of the surface plots in Figs. 2 and 3 comes  
 304 with substantial uncertainty, particularly given that the responses are nonlinear. At unusu-  
 305 ally warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;  
 306 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,  
 307 and/or prey can often be substantially different from the behaviour at typical tempera-  
 308 tures. As extreme temperature events become more frequent and prolonged (Yao *et al.*,  
 309 2022; IPCC, 2023), mammals will be increasingly forced towards atypical behaviours, which  
 310 will have the potential to substantially alter community structures and behaviours, both  
 311 during such events and afterwards (Zhang *et al.*, 2023). For instance, changes in climate and  
 312 phenology impact the life history and behaviour of many hibernating mammals (Wells *et al.*,

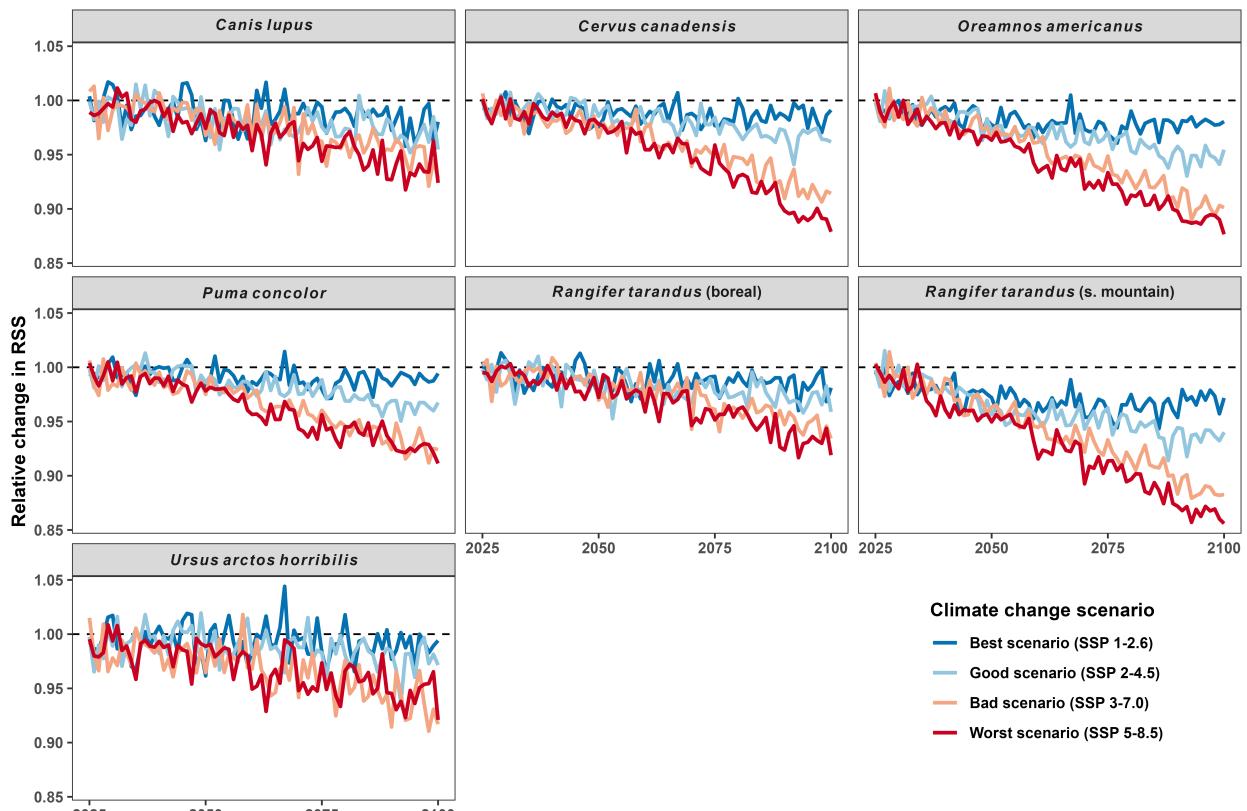
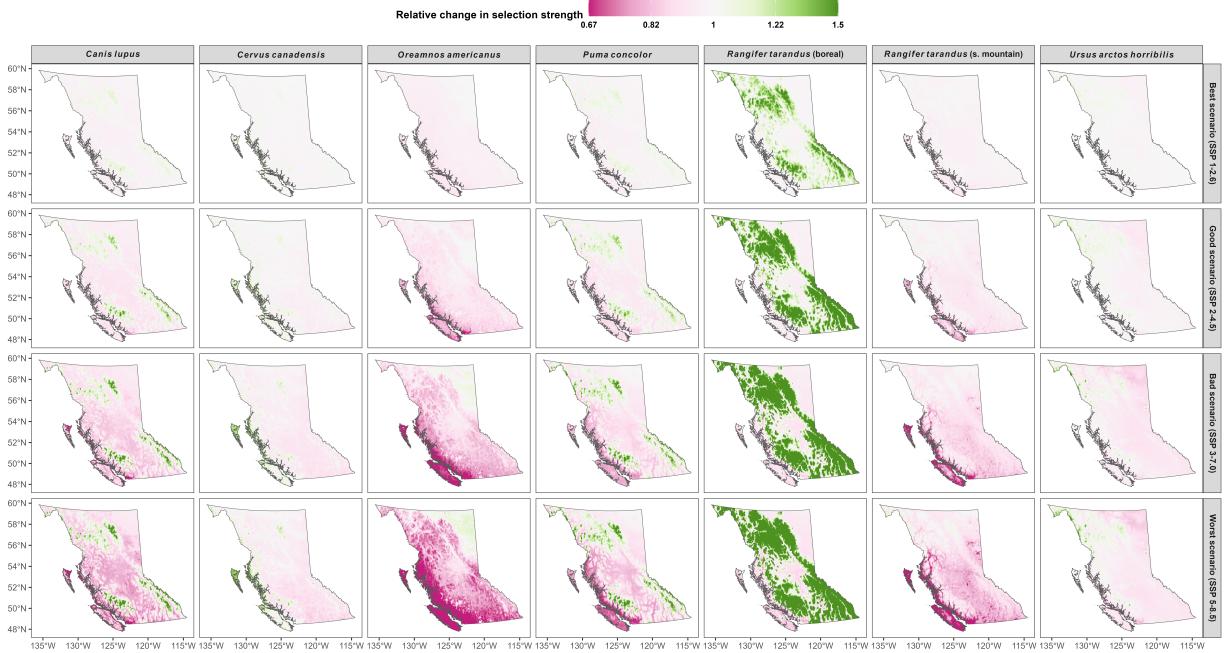


Figure 6: **All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario.** Lines indicate the projected change in RSS for the bottom 5%, median, and top 5% RSS values within the species' current extent. Changes are relative to the mean RSS for each quantile in 2025 across the four Shared Socioeconomic Pathways (SSPs).



**Figure 7: Climate change will impact each species' habitat relative selection strength (RSS) differently.** The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the  $\log_2$  scale to help visualize patterns in doubling, and values are capped to 0.67 and 1.5 ( $\approx 2^{\pm 0.6}$ ; original data ranged 0.26 to 117). The increase in boreal caribou's RSS for high elevations at warmer temperatures was highly uncertain and often not credible at the 95% level.

313 2022), and hot weather can also affects mammals' sleep quality (e.g., wild boars, *Sus scrofa*:  
 314 Mortlock *et al.*, 2024) and likelihood to enter torpor (e.g., Australian eastern long-eared  
 315 bat, *Nyctophilus bifasciatus*: Fjelldal, Wright & Stawski, 2021). Our results show that warmer  
 316 temperatures cause grizzly bears to move further earlier in the year (Fig. 2), which may  
 317 alter the frequency and intensity of human-wildlife conflict, especially with the addition of  
 318 growing pressures from human development and presence (Sih *et al.*, 2011; Johnson *et al.*,  
 319 2018; Weststrate *et al.*, 2024). At the same time, warmer winters may reduce mammals'  
 320 energetic expenditure (Berger *et al.*, 2018; Schmidt *et al.*, 2020), increase their chances of  
 321 finding food or being predated upon (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*,  
 322 2021; Slatyer, Umbers & Arnold, 2022; Sullender *et al.*, 2023), and affect the timing and  
 323 duration of migrations (Sawyer *et al.*, 2009; Xu *et al.*, 2021; Leclerc *et al.*, 2021) as well as  
 324 the overall ease of movement as snow cover and depth decrease (Leclerc *et al.*, 2021; Melin *et*  
 325 *al.*, 2023). These changes will likely have complex consequences for population and ecosys-  
 326 tem structures and dynamics as prey, predators, and competitors experience altered seasonal

cycles and increasingly common climate “weirding” (Bunnell *et al.*, 2011), including warmer temperatures and more frequent and intense extreme events (Yao *et al.*, 2022; IPCC, 2023), such as heat waves, cold spells, floods and droughts, plant and animal die-offs, and sudden growth surges (sometimes referred to as “black swan” events – see: Logares & Nuñez, 2012; Anderson *et al.*, 2017).

Our ability to respond to current and future changes in climate is contingent on our ability to prepare for and predict change. However, predicting animal behaviour becomes increasingly complicated as the conditions animals are exposed to deviate from current, typical conditions, especially when responses are nonlinear and data are sparse. Consequently, we do not present our results as a definitive guide to how mammals in BC will respond to climate change. Instead, we hope they serve as a starting point to (1) demonstrate that mammals’ movement rates and habitat selection depend on temperature and (2) how one can estimate mammals’ changes in movement behaviour due to climate change. An important limitation of Figs. 2 and 3 is that we do not include measures of uncertainty around the estimated responses, as they cannot be incorporated easily in surface plots, and the purpose of the figures was to illustrate the magnitude and direction of the responses rather than contrasting the surfaces against some hypotheses. Still, we stress that uncertainty is crucial in producing transparent and informed results, particularly when using such estimates for decision-making or predicting future changes, as we do in Figs. 4 and 6. We present the spatial estimates of distance traveled and relative habitat selection strength in 2100 without measures of uncertainty for conciseness, but we suggest that future studies and reports include some form of compatibility intervals (Gelman & Greenland, 2019), whether these be Bayesian Credible intervals (McElreath, 2020) or Frequentist Confidence Intervals, although the latter do not provide a measure of uncertainty in the common sense of the word (Morey *et al.*, 2016; Amrhein, Greenland & McShane, 2019). As alternatives to heat-map surface plots, one may include compatibility intervals using faceted or perspective plots of the surfaces along with the intervals (e.g., Fig. 5 in Akkaya Hocagil *et al.*, 2024) or overlapping

<sup>354</sup> contour plots on the surfaces (e.g., Fig. 4.14 on page 187 of Wood, 2017). For a simpler  
<sup>355</sup> figure, one could also include lines with compatibility intervals for the responses at different  
<sup>356</sup> temperatures.

<sup>357</sup> How to represent uncertainty may seem esoteric, but communicating uncertainty is cru-  
<sup>358</sup> cial in assessing risk probabilistically (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado &  
<sup>359</sup> Brechmann, 2014). Recent events in global politics, including global conflicts (McNutt &  
<sup>360</sup> Hildebrand, 2022; Tollefson, 2022) and the rapid rise in generative machine learning (also  
<sup>361</sup> referred to as artificial intelligence and GenAI, see Roumeliotis & Tselikas, 2023; Van Noor-  
<sup>362</sup> den & Webb, 2023; DeepSeek-AI *et al.*, 2025) and its prohibitive energy and water demands  
<sup>363</sup> (Li *et al.*, 2023) and carbon footprint (Luccioni, Viguier & Ligozat, 2024), have placed doubt  
<sup>364</sup> on the likelihood and feasibility of reaching climate change goals that seemed achievable in  
<sup>365</sup> the past decade (United Nations Environment Programme *et al.*, 2024). Maintaining global  
<sup>366</sup> warming below 1.5 or even 2.0°C has been questioned (United Nations Environment Pro-  
<sup>367</sup> gramme *et al.*, 2024), and mitigating climate change will require extensive and widespread  
<sup>368</sup> collaborative effort (e.g., Huang & Zhai, 2021). Similarly, protecting a third of the world's  
<sup>369</sup> terrestrial and aquatic ecosystems (Section H, Targets 2 and 3 of Convention on Biological  
<sup>370</sup> Diversity, 2022) appears less tangible as global political and environmental conditions change  
<sup>371</sup> rapidly and unpredictably (Sih *et al.*, 2011; Simmons, Nolte & McGowan, 2021; Guenette,  
<sup>372</sup> Kenworthy & Wheeler, 2022; Sovacool, Baum & Low, 2023), and achieving such a goal will  
<sup>373</sup> require active collaboration with local Peoples, especially Indigenous Peoples (Wong *et al.*,  
<sup>374</sup> 2020; Lamb *et al.*, 2023). Understanding the consequences of climate change on mammals'  
<sup>375</sup> movement behaviour and spatial distribution (Williams & Blois, 2018) is a first step towards  
<sup>376</sup> anticipating and proactively responding to future changes in human-induced rapid environ-  
<sup>377</sup> mental change (Sih *et al.*, 2011), including climate change. In the following sections, we  
<sup>378</sup> discuss the implications of our results in more detail. We then expand on consequences for  
<sup>379</sup> conservation during the 21<sup>st</sup> century and considerations for future studies.

380 **4.1 Effects of temperature on movement rates**

381 The lack of common effects of temperature across all species' movement rates indicates that  
382 responding to current conditions and preparing for future changes will require a variety of  
383 physiological and behavioral adaptations as ecological communities respond in complex and  
384 interconnected ways. Although our models do not account for any physiological or explicit  
385 phenological changes, the tensor product terms in Fig. 2 suggest that warmer temperatures  
386 cause many species to alter their daily and seasonal activity patterns (most visible in pumas  
387 and grizzly bears). For example, when temperatures were above 0°C, pumas moved most  
388 at night, but when temperatures were below 0°C they tended to move more throughout  
389 the day. Throughout the year, they adapted their tolerance to temperature and moved less  
390 when it was relatively hot (for a given time of year), especially in spring and summer. The  
391 strong reduction in wolves', elk's, pumas', and boreal caribou's mid-day movement rates  
392 when summer temperatures are above 20°C suggests that the increasingly common and  
393 intense heat waves across British Columbia will have community-wide impacts on movement  
394 rates, encounter rates, and potentially community structure (Martinez-Garcia *et al.*, 2020).  
395 More work is necessary on interspecific responses to temperature, including the effects of  
396 temperature on predation rates (Glass *et al.*, 2021; but see: Cunningham, Gardner & Martin,  
397 2021; Brivio *et al.*, 2024). As indicated by grizzly bears' tendency to travel greater distances  
398 earlier in the year with increasing temperatures, the increase in intensity and frequency  
399 of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the  
400 occurrence and timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range  
401 expansions (Morley, 2021; Malpeli, 2022; Carbeck *et al.*, 2022). However, not all species may  
402 be able to adapt at the current rate of climate change (Heten *et al.*, 2014; Williams  
403 & Blois, 2018), especially since landscape changes will likely depend not only on the direct  
404 effect of temperature but also on cascading changes in the availability and unpredictability  
405 of resources (McLellan & McLellan, 2015; Pigeon, Stenhouse & Côté, 2016; Mezzini *et al.*,  
406 2025).

407 **4.2 Effects of temperature on habitat selection**

408 As with the effects of temperature on movement rates, the lack of common effects of  
409 temperature across all species indicates that efficient and proactive habitat conservation  
410 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
411 physiological responses to temperature that may impact movement such as changes in the  
412 phenology of plants, ice, or mammalian physiology or behaviour (e.g., moulting, migration)  
413 other than as direct responses to temperature. Consequently, the behavioural changes we  
414 present should be interpreted carefully. While some seasonal cycles do not depend directly on  
415 temperature and may thus not be impacted directly by climate change (such as those driven  
416 by photoperiod, see Liu *et al.*, 2022), the predictions we present also rely on the assumption  
417 that mammals will not adapt these seasonal cycles based on temperature-dependent cues,  
418 such as weather (Xu & Si, 2019) or forage availability (Middleton *et al.*, 2018), which may not  
419 be correct. Additionally, it is important to stress the distinction between habitat selection  
420 and quality. While animals tend to select for high-quality habitats (e.g., Wright, 2024),  
421 high selection strength can also be a consequence of an ecological trap, an area animals  
422 are attracted to that provides a net loss of fitness rather than a gain (Swearer *et al.*, 2021;  
423 Zuñiga-Palacios *et al.*, 2021).

424 **4.3 Predicted changes in movement during the 21<sup>st</sup> century**

425 Achieving the goals laid out by the “30 by 30” conservation initiative (Section H, Targets 2  
426 and 3 of Convention on Biological Diversity, 2022) will require careful planning but often also  
427 rapid action. In the case of Canada, only 13.7% of its terrestrial areas and inland waters were  
428 protected at the end of 2023 (Environment and Climate Change Canada, 2024; Minister of  
429 Environment and Climate Change, 2024). Additionally, efficient and effective conservation  
430 will require collaboration with Indigenous and local communities to ensure Treaties are  
431 respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020; e.g., Falardeau *et*  
432 *al.*, 2022; Lamb *et al.*, 2023) while also actively preparing for future change (Desjardins,

<sup>433</sup> Friesen & Jordan, 2020; Hessami *et al.*, 2021). The large range in predicted changes by 2100  
<sup>434</sup> (both across species and within species' current ranges) and high spatial heterogeneity in  
<sup>435</sup> Fig. 7 highlight the need for careful planning that incorporates not only accurate estimates  
<sup>436</sup> of change but also pragmatic and communicable measures of uncertainty and variability  
<sup>437</sup> around such estimates. The width of the prediction intervals in Fig. 4 suggest that spatial  
<sup>438</sup> and intra-individual variation should be accounted for when deciding the location and size  
<sup>439</sup> of protected areas.

<sup>440</sup> Accurate estimates of the effects of changes in temperature on mammals' movement  
<sup>441</sup> require a holistic view of the direct effects of temperature on mammals' movement directly  
<sup>442</sup> as well as its effects on other drivers of movement, such as forage availability (Mezzini *et al.*,  
<sup>443</sup> 2025), population dynamics (**needs\_ref?**), competitive pressure (e.g., Tórrez-Herrera, Davis  
<sup>444</sup> & Crofoot, 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great  
<sup>445</sup> variation among the responses of different species (and individuals). As selection strength  
<sup>446</sup> for current ranges changes (and likely decreases), some animals may disperse, relocate to a  
<sup>447</sup> new habitat, or remain within the current range suffer a decrease in fitness and an increase  
<sup>448</sup> in extinction risk (Duncan *et al.*, 2012).

<sup>449</sup> Together, the predicted changes in distance traveled and habitat selection indicate that  
<sup>450</sup> climate change will have complex consequences for populations as well as cascade effects  
<sup>451</sup> within ecosystems as species adapt to the changing environments (or fail to do so: Botero  
<sup>452</sup> *et al.*, 2015; Polazzo *et al.*, 2024). The resulting changes in mammalian movement be-  
<sup>453</sup> haviour will have ramifications in individuals' encounter rates (Martinez-Garcia *et al.*, 2020;  
<sup>454</sup> e.g., Hou *et al.*, 2020), population dynamics (**needs\_ref?**), and food webs (**needs\_ref?**)  
<sup>455</sup> as landscapes change and animals face increasing pressures from human activity (Sih *et*  
<sup>456</sup> *al.*, 2011; Tucker *et al.*, 2018), including habitat fragmentation (**needs\_ref?**), habitat loss  
<sup>457</sup> (**needs\_ref?**), and greater human presence in wild spaces (Rice, 2022; Rosenthal *et al.*,  
<sup>458</sup> 2022; Weststrate *et al.*, 2024).

459 **4.4 Considerations for future studies**

460 Our work highlights three central considerations for future research: (1) telemetry sam-  
461 pling rates should be designed primarily in relation to the movement timescales of the species  
462 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of in-  
463 dividuals tracked and the length of each telemetry should depend not just on population  
464 size but also environmental stability, and (3) predicting changes in movement behaviour  
465 becomes highly complex when responses are nonlinear, especially when changes depend on  
466 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses  
467 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020). We  
468 address each consideration in the following three paragraphs.

469 While the `ctmm` models produced scale-independent estimates of speed (i.e., model inter-  
470 pretation is independent of sampling interval: Noonan *et al.*, 2019a), the accuracy, size, and  
471 stability of speed estimates still depended on the GPS sampling frequency. This is because  
472 coarsely-sampled movement data contains information on large-scale movements (e.g., range  
473 crossings, migrations) but not fine-scale movements (e.g., first-order habitat selection *sensu*  
474 Johnson, 1980; also see Nathan *et al.*, 2022). Using the boreal caribou as an example, the  
475 13-hour sampling interval allows us to reasonably estimate the caribou's movement path at  
476 a temporal scale of approximately 13 hours (or greater), but we cannot produce reasonable  
477 movement trajectories at a much finer (e.g., hourly) scale. Consequently, we suggest being  
478 cautious when comparing estimated movement behaviours across species, even though all  
479 predictions have been corrected to the hourly timescale by predicting for 1-hour time inter-  
480 vals (i.e., `dt_hours = 1`). Thus, sampling schedules should be fine enough to reconstruct  
481 animals' movement at a sufficiently fine scale. Good estimates of an animal's speed and its  
482 movement path require telemetry locations to be taken more often than the animal's direc-  
483 tional persistence (Noonan *et al.*, 2019a), so that, on average, the dataset contains multiple  
484 locations in between changes in direction. What constitutes a change in direction depends  
485 on what movement scale one is investigating. Small-scale movements and first-order spa-

486 tial selection will require more frequent sampling than migratory movement or second- and  
487 third-order spatial selection. While `ctmm` movement models are scale-invariant in that any  
488 model can be scaled to larger or smaller areas and timescales, the model estimates are not  
489 independent of the scale of the sampling frequency.

490 When landscapes are relatively predictable across years, a larger number of sampled in-  
491 dividuals is likely preferable over longer, multi-year telemetries. This allows one to quantify  
492 the variance across individuals, including the range of conditions and environments that  
493 individual animals are in. A good estimate of inter-individual variance provides better co-  
494 efficient estimates along with more appropriate measures of uncertainty. However, when  
495 conditions across years are relatively stochastic, multi-year telemetries allow one to better  
496 estimate inter-annual variation without conflating it with inter-individual differences. In  
497 either case, carefully-designed sampling schedules and (Bayesian) hierarchical models can  
498 provide good estimates of the effects of interested along with appropriate measures of un-  
499 certainty (McElreath, 2020).

500 Quantifying and communicating uncertainty become particularly important as we predict  
501 for conditions for which we have little to no data, such as during extreme events. Addition-  
502 ally, estimating nonlinear trends is particularly difficult near the edges of the data (e.g.,  
503 extremely high temperatures), especially when data is scarce. Consequently, the estimated  
504 responses at the fringes of the surfaces in figures 2 and 3 are more likely likely to be poorly  
505 estimated, particularly in the case of HRSFs, but increasing data density throughout the  
506 resource-temperature surfaces can ameliorate the issue. Preparing for future changes re-  
507 quires some degree of inevitable risk, so it is imperative that models be statistically sound  
508 and interpretable, and that results are communicated transparently and clearly to decision  
509 makers and the public alike.

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