

Predicting how climate change will affect how and where terrestrial  
mammals will move

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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 fitness, habitat selection, and community structure. Previous studies have quantified the effects of temperature on mammalian movement behaviour, but few have quantified the effects of future climate change. Consequently, it is still unclear how and where mammals will move in the 21<sup>st</sup> century. We address this gap by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on the probability of moving, the speed when moving, and the habitat selection of six species throughout British Columbia, Canada. We show that temperature is a strong determinant of when, how, and where mammals move, and that climate change will impact mammals' movement rates and habitat selection throughout the 21<sup>st</sup> century. We found no common effects of temperature on the species' movement rates, so we suggest that species' estimated responses be interpreted jointly when making inferences about how climate change will impact ecological communities. In contrast, habitat selection strength decreased for all species within their current ranges, suggesting that all six species will shift their range in the coming decades. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behavior and community structure will become crucial for effective and proactive conservation. We thus conclude by providing suggestions for conservation and future research while calling for a more holistic and collaborative framework.

## <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 *et al.*, 1992), optimize habitat use (Winter *et al.*, 2024), and escape  
<sup>5</sup> predation (Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). However,  
<sup>6</sup> ambient temperature affects mammals' movement rates by altering the energetic cost of  
<sup>7</sup> movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn  
<sup>8</sup> & Seebacher, 2022), the ease of movement (e.g., snow depth and density, see Montgomery  
<sup>9</sup> *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and the risk of overheating (Heten  
<sup>10</sup> *et al.*, 2014; Dyer *et al.*, 2023). Animals may search for a short-term buffer from extreme  
<sup>11</sup> heat or cold via thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*,  
<sup>12</sup> 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), which may even be preferred over  
<sup>13</sup> forage abundance (e.g., Hall *et al.*, 2016). Additionally, temperature also affects movement  
<sup>14</sup> indirectly through other drivers of movement behaviour, such as trophic interactions (Hegel *et*  
<sup>15</sup> *al.*, 2010). Changes in temperature thus affects how animals move (e.g., movement frequency  
<sup>16</sup> and speed – their movement behaviour: Nathan *et al.*, 2008; Dyer *et al.*, 2023) and where  
<sup>17</sup> they move to (i.e., their habitat selection: Merkle *et al.*, 2016; Alston *et al.*, 2020; Giroux *et*  
<sup>18</sup> *al.*, 2023).

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

27 temperature, phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to  
28 respond within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016;  
29 Xu *et al.*, 2021).

30 In the last 200 years, many ecosystems experienced widespread warming that resulted  
31 in milder and shorter winters, hotter and longer summers, and a greater risk of extremely  
32 high temperatures and severe forest fires (IPCC, 2023; Zurowski, 2023). Over the next  
33 100 years, these changes are expected to worsen and continue to impact mammals' fitness,  
34 movement behaviour, and habitat selection as animals cope with growing heat stress (Deb *et*  
35 *al.*, 2020; Woo-Durand *et al.*, 2020) and more frequent and intense extreme events (Bunnell  
36 *et al.*, 2011), along with increasing anthropogenic pressure (Sawyer *et al.*, 2009; Sih *et al.*,  
37 2011; Weststrate *et al.*, 2024). Consequently, it remains unclear how or whether species  
38 will be able to respond to climate change in the current century (Deb *et al.*, 2020; Woo-  
39 Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially when populations fail to adapt to  
40 changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable to do so  
41 (Sherwood & Huber, 2010; Williams & Blois, 2018). Uncertainty in future conditions and  
42 their consequences on ecosystems present a need for a comprehensive understanding of (1)  
43 the direct effects of temperature on animal movement behaviour and (2) the implications this  
44 will have on populations and species' adaptability and resiliency, community structure, and  
45 biodiversity at large. Recent work has documented the effects of climate change on mammals'  
46 ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation  
47 (Mota-Rojas *et al.*, 2021), and trait-based responses (McCain, 2019), but it is still unclear  
48 how mammals will adapt their small-scale movement and habitat selection to changes in  
49 temperature during the 21<sup>st</sup> century (IPCC, 2023; but see Hetem *et al.*, 2014; Winter *et al.*,  
50 2024).

51 Understanding the direct and indirect impacts of temperature on mammalian movement  
52 is essential for decision makers to be able to prepare for and respond to change in a proac-  
53 tive manner (e.g., Sawyer *et al.*, 2009; McCain, 2019). The Canadian province of British

54 Columbia is currently experiencing rapid widespread warming (Turner & Clifton, 2009; Dier-  
55 auer *et al.*, 2021), phenological shifts (Basu *et al.*, 2024; e.g., Tysor, 2025), and more frequent  
56 and intense extreme events (e.g., Zhang *et al.*, 2023), including forest fires (Zurowski, 2023).  
57 As we approach the deadline for the “30 by 30” conservation initiative, a global effort to  
58 conserve 30% of the world’s lands and oceans by 2030 (Section H, Targets 2 and 3 of Con-  
59 vention on Biological Diversity, 2022), decision makers must understand which areas will be  
60 of greatest value for maximizing the project’s effectiveness. Predicting how climate change  
61 will affect how, when, and where animals will move is necessary for identifying which land-  
62 scapes are most valuable now as well as in the future. Failing to understand how changes in  
63 temperature will affect mammalian movement behaviour and habitat selection will hinder  
64 our ability to respond to the current climate crisis and make decisions that are viable in the  
65 long term.

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

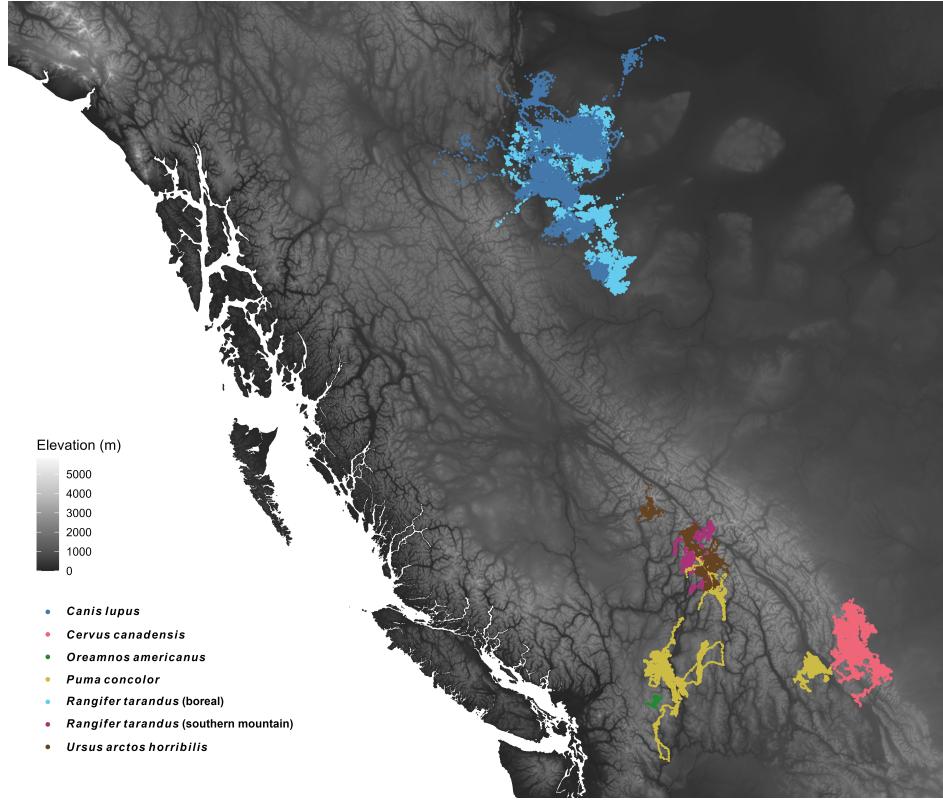


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Start and end of the GPS telemetries 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
<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

78 **2 Methods**

79 **2.1 Datasets used**

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

86 **2.1.1 GPS telemetry data**

87 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
88 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou  
89 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public BC Oil and  
90 Gas Research and Innovation Society repository ([https://www.bcgoris.ca/projects/boreal-](https://www.bcgoris.ca/projects/boreal-caribou-telemetry-data)  
91 [caribou-telemetry-data](https://www.bcgoris.ca/projects/boreal-caribou-telemetry-data)). **MISSING INFO ON OTHER TELEMETRY DATA.**  
92 From the full set of telemetry data, a total of 2396 GPS locations (0.16%, including col-  
93 lar calibration data) were removed using diagnostic plots of (1) distance from the median  
94 location, (2) straight-line displacement between locations, (3) turning angle, and (4) time  
95 interval between consecutive points. Particular attention was paid to points with large turn-  
96 ing angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially if antecedent  
97 and subsequent points indicated stationary behaviour. See Appendix A for additional infor-  
98 mation.

99 **2.1.2 Historical and projected temperature data**

100 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset  
101 (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting

102 server (ECMWF; [www.ecmwf.int](http://www.ecmwf.int); <https://cds.climate.copernicus.eu>). Proximal tempera-  
103 ture was estimated for each location by extracting the value from the corresponding raster  
104 cell from the temporally nearest raster using the `extract()` function from the `terra` package  
105 (version 1.7-46, Hijmans, 2023) for R (R Core Team, 2024).

106 We obtained rasters of projected monthly average temperature at a  $0.08^\circ$  resolution in BC  
107 from 2020 to 2100 under the different SSPs via the `climatenetR` package (version 1.0, Burnett,  
108 2023) for R. Since the climate projections only provided monthly means and ranges but no  
109 measures of variance or distributional assumptions, we used the hourly ERA5 data for BC  
110 from 1998 to 2023 (extremes included, see Hersbach *et al.*, 2023) to calculate within-month  
111 variance in temperature, which we defined as the variance within a given pixel, month, and  
112 year. We then modeled the estimated variance using a GAM for location and scale (GAMLS,  
113 see: Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017).  
114 The linear predictor for the location (i.e., the mean) included smooth terms of the within-  
115 pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-  
116 dimensional smooth of space, and a tensor interaction product term of space and month. The  
117 linear predictor for the scale term (which governs the mean-variance relationship) included  
118 smooth terms of the monthly mean, month, and space. We did not include a smooth of year  
119 to avoid unrealistic projections when extrapolating beyond the range of historical data.

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

128 **2.1.3 Resource rasters**

129 We estimated percent forest cover and distance from water using the rasters created by  
130 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
131 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
132 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
133 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover  
134  $> 0\%$ ) or without water (cover = 0%) and then calculated each pixel's distance from the  
135 nearest pixel with water using the `distance()` function from the `terra` package. Finally,  
136 we obtained two digital elevation models using the `get_elev_raster()` function from the  
137 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom  
138 of 6 ( $0.009^\circ$ ) for model fitting and one with a zoom of 3 ( $0.08^\circ$ ) for downloading climate  
139 change projections via `climatenar`. All final rasters and code are available on GitHub at  
140 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

141 **2.2 Estimating mammals' instantaneous speeds**

142 We modeled each animal's movement using continuous-time movement models (Fleming *et*  
143 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then  
144 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all  
145 models with finite speed estimates (415 of 433, see Fleming *et al.*, 2014; Noonan *et al.*,  
146 2019a). The 18 animals with insufficiently fine sampling were for one mountain goat, 15  
147 boreal caribou, and 2 southern mountain caribou (Table 1).

148 Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-  
149 gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
150 minimum instantaneous speed could be 0. We performed this correction by subtracting  
151 each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
152 used is available on GitHub at [https://github.com/QuantitativeEcologyLab/bc-mammals-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

154 small, non-zero speeds, we determined whether an animal was moving or not using the in-  
155 flexion point of each species' histogram of detrended speed estimates, as  $k$ -nearest neighbors  
156 did not discriminate between states well (Fig. B3).

### 157 2.3 Estimating the effects of temperature on mammals' movement

158 The following sections detail the statistical framework and modelling we used to estimate  
159 the effect on temperature on mammals' movement. To assess the importance of including  
160 temperature as an explicit covariate (rather than including its effects with time of day and  
161 day of year), we fit models with and without smooth effects of temperature and compared  
162 the fits of the two sets of models. We provide the relevant Directed Acyclical Graphs in the  
163 Appendix (Figs. B1-B2).

#### 164 2.3.1 Disentangling direct and indirect effects

165 In this study, we separate the effects of temperature on mammalian movement into indirect  
166 and direct effects. We call "indirect" all effects that can be intervened on by altering an  
167 animal's habitat (its geographic space *sensu* Matthiopoulos, 2022), and we refer to all other  
168 effects as "direct". For example, an increase in temperature may push an animal to prefer  
169 higher forest cover in search of shade, and conservationists can thus mitigate these indirect  
170 effects of temperature on movement behaviour by increasing the availability of forested ar-  
171 eas, since the effect of temperature on movement is conditional on forest cover availability.

172 In contrast, the animal may avoid moving if temperatures are above 35°C, irrespective of  
173 its geographic and environmental space (*sensu* Matthiopoulos, 2022), so it is not possible to  
174 mitigate the effects of temperature on movement behaviour (other than changing tempera-  
175 ture directly). We provide the relevant Directed Acyclical Graphs in the Appendix (Figs.  
176 B1-B2).

<sup>177</sup> **2.3.2 Effects of temperature on movement rates**

<sup>178</sup> We estimated the effects of temperature ( $^{\circ}\text{C}$ ) on mammals' movement state (moving or not)  
<sup>179</sup> and speed when moving using two Hierarchical Generalized Additive Models (HGAMs, see  
<sup>180</sup> Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version 1.9-1,  
<sup>181</sup> Wood, 2017). The first HGAM estimated the probability that an animal was moving,  $P(M)$ ,  
<sup>182</sup> with a binomial family of distributions and logit link function. The response variable `moving`  
<sup>183</sup> was coded as 1 if moving and 0 if not. The second HGAM estimated an animal's speed when  
<sup>184</sup> moving (`speed`) with a gamma family of distributions and log link function. The HGAMs  
<sup>185</sup> included random intercepts for each animal (`s(animal, bs = 're')`), fixed-effect intercepts  
<sup>186</sup> for each species (`species`), and species-level by smooths (`s(..., by = species)`), which  
<sup>187</sup> allowed each species' term to be estimated independent of other species (see model I in Figure  
<sup>188</sup> 4 of Pedersen *et al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific  
<sup>189</sup> Daylight Time; `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). Additionally, the  
<sup>190</sup> models had three tensor product interaction terms (`ti()`) by each species: (1) day of year  
<sup>191</sup> and time of day, (2) temperature and time of day, and (3) temperature and day of year.  
<sup>192</sup> These three terms accounted for: (1) seasonal changes in day length, (2) hourly changes  
<sup>193</sup> in the response to temperature (e.g., changes in nocturnality), and (3) seasonal changes in  
<sup>194</sup> the response to temperature (e.g., changes in coats and migration timing). Finally, smooth  
<sup>195</sup> terms of log-transformed hours between GPS locations (`dt`) accounted for irregular sampling  
<sup>196</sup> rates. A global term of `log(dt)` accounted for the overall effect of sampling interval, while  
<sup>197</sup> a factor-smooth interaction term (`s(log(dt), species, bs = 'fs')`) allowed for species-  
<sup>198</sup> level deviations from the global term while assuming a common smoothness parameter across  
<sup>199</sup> species (see model GS in Figure 4 of Pedersen *et al.*, 2019). The HGAMs accounted for the  
<sup>200</sup> cyclicity of time of day and day of year using cyclic cubic splines (`bs = 'cc'`; see p. 202  
<sup>201</sup> of Wood, 2017). Together, the binomial HGAM and the gamma HGAM inform us on an  
<sup>202</sup> animal's long-term average speed, since it is the product of the probability of moving and  
<sup>203</sup> its average speed when moving. We fit the models with fast Restricted Maximum Likeli-

204 hood ('fREML') and discretized covariates (`discrete = TRUE`) to optimize computational  
 205 efficiency with no appreciable losses to model performance (Wood *et al.*, 2015, 2017; Li &  
 206 Wood, 2020). Additional details are provided in Appendix B.

```
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)))
```

### 207 2.3.3 Effects of temperature on habitat selection

208 We estimated the effects of temperature on each species' selection for percent forest cover  
 209 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 210 ting a Hierarchical Resource Selection Function for each species using an HGAM with a Pois-  
 211 son family of distributions and log link function (Appendix B, also see Aarts *et al.*, 2008).  
 212 We accounted for the spatiotemporal autocorrelation in the telemetry locations by weighting  
 213 each point based on the telemetry's Autocorrelated Kernel Density Estimate (Fleming &  
 214 Calabrese, 2017; Noonan *et al.*, 2019b) to produce estimates of second- and third-order habi-  
 215 tat selection (*sensu* Johnson, 1980). While we recognize there are other important drivers

216 of habitat selection (e.g., forest age, forest type, prey availability), we decided to only use  
 217 these three proxies to produce results that are comparable between species and to make  
 218 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)
```

219 Smooth effects of percent forest cover, elevation, and distance to water accounted for  
 220 the species-level average selection strength for each resource. A random effect for each in-  
 221 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
 222 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
 223 selection (i.e., individual-level deviations from the species-level average). Tensor interaction  
 224 product terms (`ti()`) of the three resources and temperature estimated the change in re-  
 225 source selection at different temperatures. Finally, we included marginal smooth terms of  
 226 temperature to account for species- and individual-level sampling biases over temperature  
 227 (e.g., sampling more during warm periods). Detections were weighted proportionally to their  
 228 degree of independence from other temporally proximate detections (`weights = weight` –  
 229 see Appendix B and Alston *et al.*, 2022), while quadrature points had a weight of 1. Quadra-  
 230 ture points were obtained using all raster cells in the 99.9% AKDE percentile. The number  
 231 of quadrature locations greatly outnumbered the number of observed locations (Fig. B13),  
 232 especially after accounting for weighting based on the degree of autocorrelation and the

233 number of home range crossings (Fig. B14).

### 234 3 Results

235 Data were relatively scarce for temperatures lower than  $-20^{\circ}\text{C}$  or above  $20^{\circ}\text{C}$  (Fig. B4).  
236 Species differed in overall mean probabilities of movement (range: 0.05 – 0.3), mean speed  
237 when moving (range: 0.42 – 2.7 km/day), and mean distance traveled (range: 0.04 – 0.6  
238 km/day; Table 2). Grizzly bears tended to move least often (probability of moving  $P(M) \approx$   
239 0.05), while wolves and pumas moved most often ( $P(M) \gtrapprox 0.23$ ). When moving, mountain  
240 goats and southern mountain caribou moved the slowest ( $\mathbb{E}(S|M) \approx 0.4 \text{ m/s}$ ), while wolves  
241 had the highest mean speed when moving ( $\mathbb{E}(S|M) \approx 2.7 \text{ m/s}$ ). Consequently, wolves  
242 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-stratifying 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> (b)	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus</i> (sm)	0.11	0.11	0.43	0.42	0.05	0.05
<i>U. arctos horr.</i>	0.05	0.05	0.72	0.72	0.04	0.04

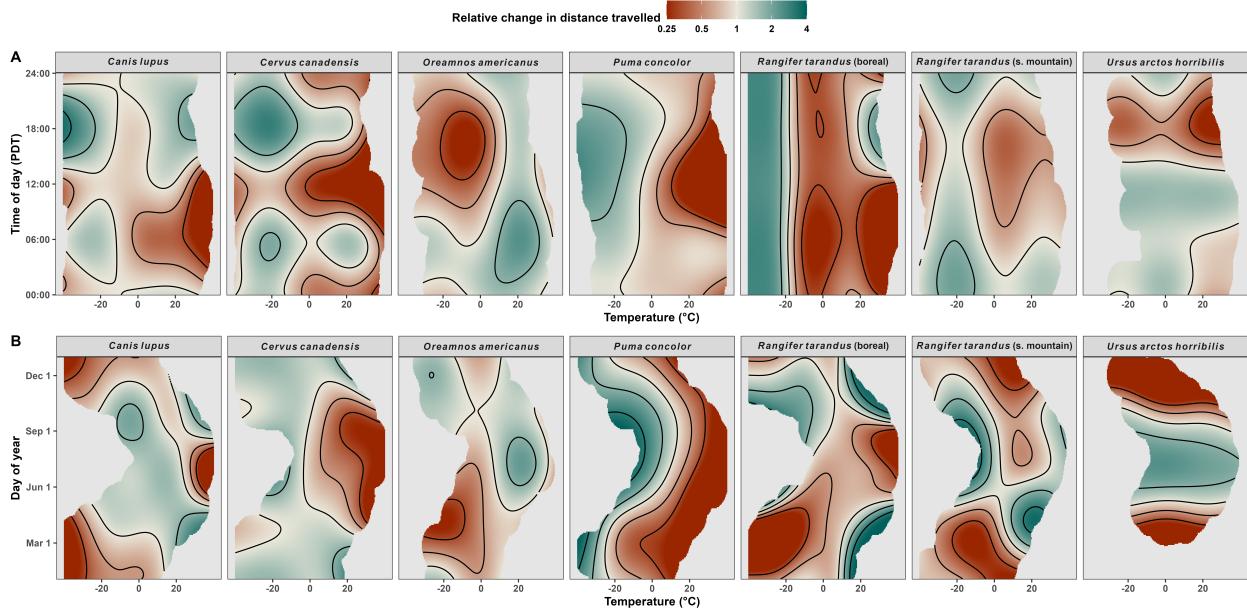
243 Near  $0^{\circ}\text{C}$ , wolves preferred dense forest cover ( $\gtrapprox 50\%$ ) high elevations, and distances  
244 from water  $< 10 \text{ km}$ ; elk preferred intermediate forest cover, elevations between 1 and 2 km,  
245 and distances from water of 5–15 km; mountain goats preferred sparse ( $< 50\%$ ) forest cover,  
246 elevations between 1 and 2 km; pumas preferred high forest cover, an elevation of  $\sim 1 \text{ km}$ ,  
247 and distances from water  $< 10 \text{ km}$ ; boreal caribou selected for intermediate to high forest  
248 cover, elevations near 500 m, and distances from water  $< 10 \text{ km}$ ; southern mountain caribou

<sup>249</sup> selected for dense forest cover, elevations near 2 km, and distances from water < 5 km; and  
<sup>250</sup> grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances  
<sup>251</sup> from water < 2 km.

<sup>252</sup> There was relatively strong agreement between models with and without temperature  
<sup>253</sup> (Figs. B5 and S13), but including temperature always resulted in better fits. All analyses  
<sup>254</sup> of deviance showed that temperature significantly affected movement behavior (all p-values  
<sup>255</sup>  $< 2.2 \times 10^{-16}$ ; all  $\Delta AIC \geq 342$ ; see Table B1 and the analyses of deviance in Appendix B).  
<sup>256</sup> The only exception to this was the mountain goat HRSF, where the addition of tempera-  
<sup>257</sup> ture resulted in a simpler model (lower model degrees of freedom) that fit the data better  
<sup>258</sup> (lower deviance), and hence no test was necessary to show that the inclusion of temperature  
<sup>259</sup> produced a better fit.

### <sup>260</sup> 3.1 Effects of temperature on movement rates

<sup>261</sup> The effects of temperature on movement rates varied in both direction and magnitude across  
<sup>262</sup> species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
<sup>263</sup> migration, hibernation; see Figs. B6-B8). Smooth interaction terms were well-behaved and  
<sup>264</sup> indicated clear shifts in activity over time of day and day of year for all species. The models  
<sup>265</sup> explained reasonably high proportions of the deviance (10.7% for the binomial model and  
<sup>266</sup> 79.3% for the Gamma model) and had good in-sample prediction (Fig. B9). All species  
<sup>267</sup> adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 2).  
<sup>268</sup> For example, wolves, elk, pumas, and boreal caribou reduced their mid-day and summer  
<sup>269</sup> movement rates when temperatures were above 20°C. However, uncertainties around the  
<sup>270</sup> estimated effects were often higher at extreme temperatures due to data scarcity. All species'  
<sup>271</sup> estimated probability of moving decreased with sampling intervals approximately above 1  
<sup>272</sup> hour, and most species' estimated speed when moving decreased monotonically with sampling  
<sup>273</sup> interval, although the estimated trends were highly uncertain for some species (Fig. B10).



**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  $2^{\pm 2}$  for ease of readability.

### 274 3.2 Effects of temperature on habitat selection

275 Species' relative selection strength (RSS) was generally strongest for elevation and weak-

276 est for forest cover, but species' RSS for resources depended on temperature. Changes in

277 RSS with temperature were also strongest for elevation and generally weakest distance from

278 water, but there were no common trends across all species for any of the three resources.

279 All species, with the exception of pumas, exhibited a clear temperature-dependent shift

280 in their preference for forest cover. At higher temperatures, wolves, mountain goats, and

281 grizzly bears became less selective for forest cover, while elk and caribou shifted towards

282 more intermediate forest cover without much of a change in preference width. All species

283 shifted elevationally with temperature, although boreal caribou did not exhibit as strong

284 of a change. As temperatures rose, elk, mountain goats, and pumas increased in elevation,

285 while boreal wolves, southern mountain caribou, and grizzly bears decreased in elevation.

286 Most species generally remained within 5 km of water, and temperature did not affect their

287 selection strength as much as for the other two resources. Again, estimated RSS values were

288 generally most uncertain at extreme temperatures (Fig. B13).

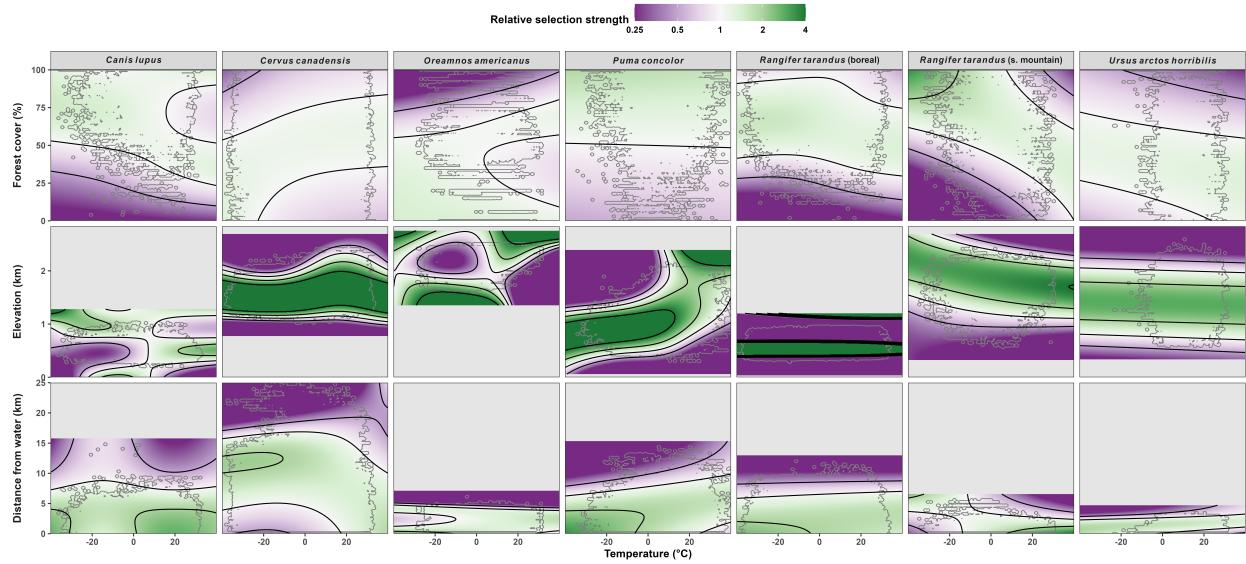


Figure 3: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were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

### 289 3.3 Predicted changes in movement during the 21<sup>st</sup> century

290 Species varied in both the direction and magnitude of predicted change in distance traveled,  
 291 but worse climate-change scenarios always corresponded to greater absolute changes in be-  
 292 haviour (Figs. 4, S11, and S12). Under the best-case scenario, absolute changes by 2100  
 293 were small (approximately 0% to 4%), while under the worst-case scenario absolute changes  
 294 ranged from  $\sim 2\%$  (grizzly bear) to  $\sim 25\%$  (pumas), although the models did not explicitly  
 295 account for changes in hibernation phenology. Throughout BC (Fig. 5), all species showed  
 296 little to no absolute change under the best-case scenario (approximately 0-4% relative to  
 297 2025, on average), and approximately 2-25% average absolute change under the worst-case  
 298 scenario, but the predicted changes varied spatially due to heterogeneity in climate change.  
 299 Again, absolute changes were smallest under the best-case scenario and greatest under the  
 300 worst-case scenario for all species.

301 All species exhibited a decrease in RSS within their current range, irrespective of climate  
 302 change scenario. Changes were often were only between -1% and -3% under the best-case  
 303 scenario but they ranged from -8% to -14% under the worst-case scenario (6). As with

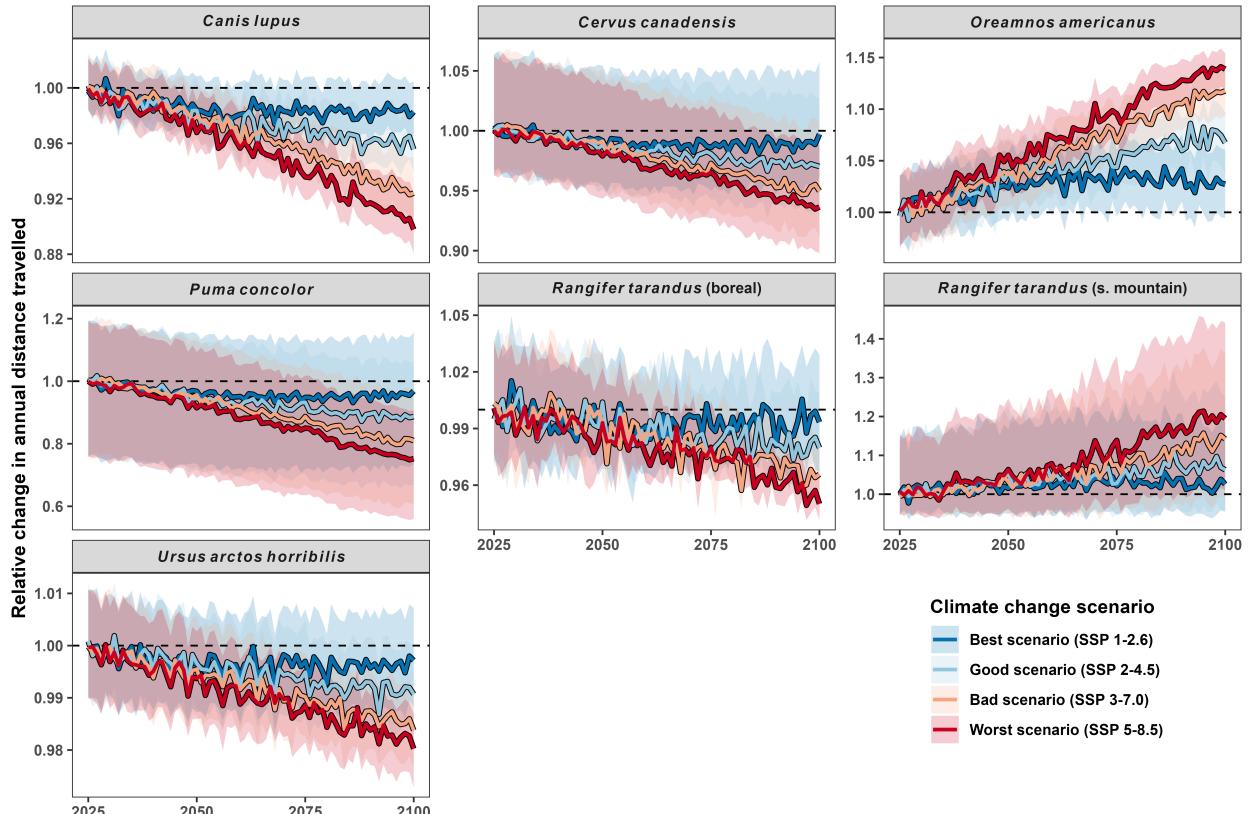
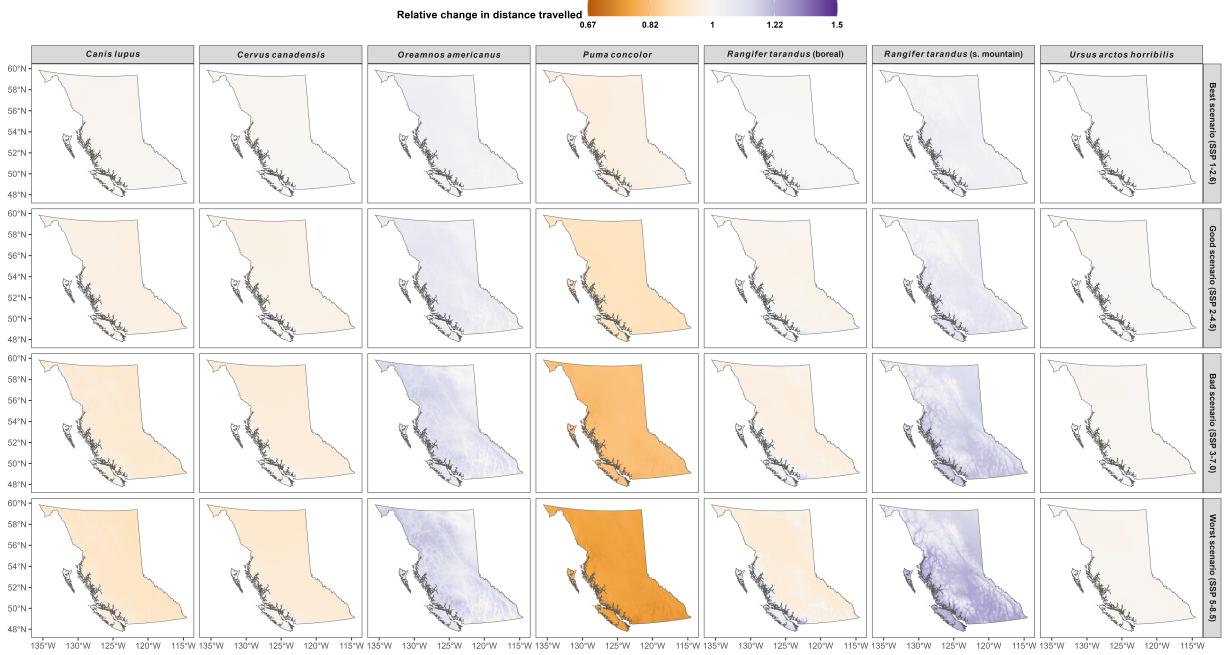


Figure 4: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes 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.

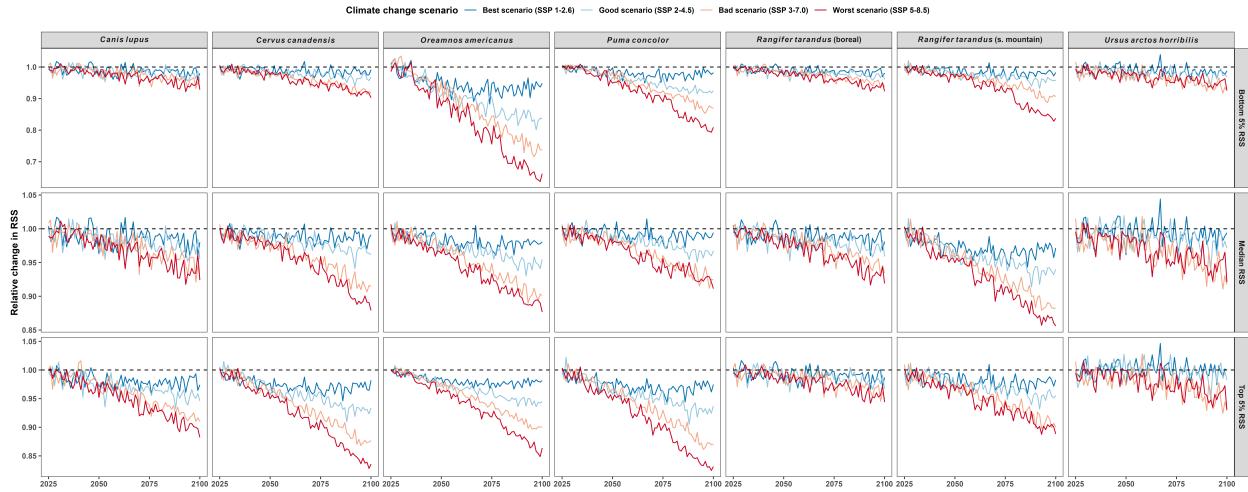


**Figure 5: Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values  $< 1$  indicate a decrease, 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 0.67 and 1.5 ( $\approx 2^{\pm 0.585}$ ; 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.

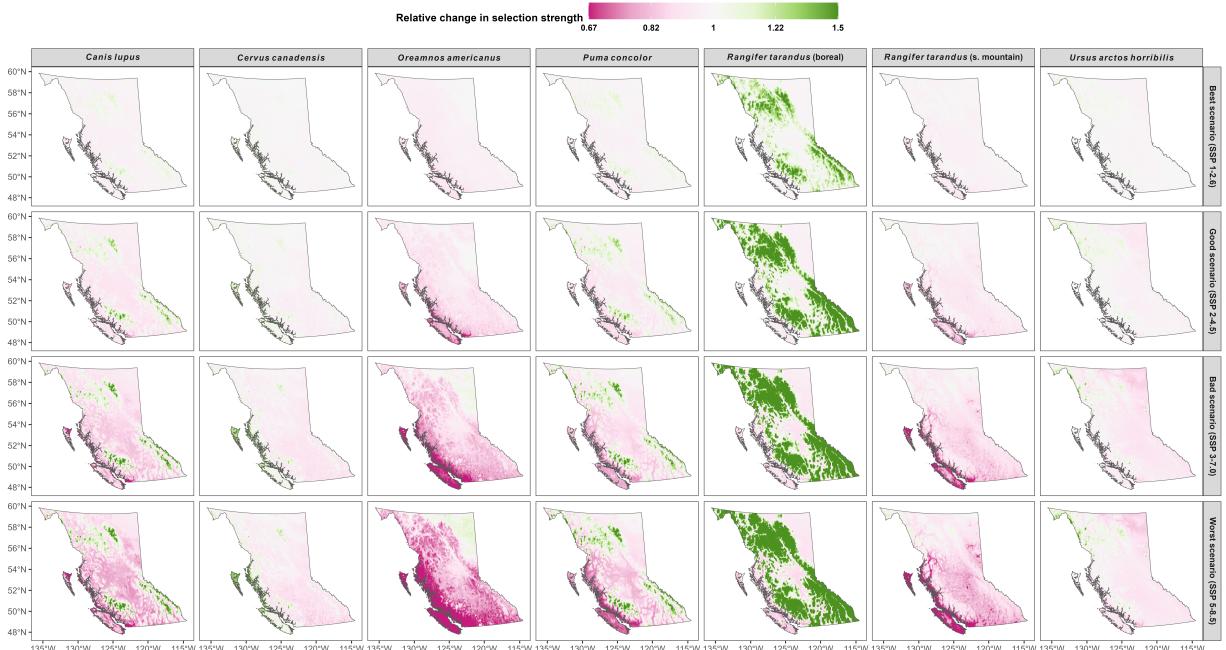
304 distance traveled, the change in RSS in 2100 varied throughout BC for all species (Fig. 7).  
 305 All species were predicted to exhibit a decrease in RSS throughout most of BC, with the  
 306 exception of boreal caribou, which had a predicted increase in approximately 67% of the  
 307 province, including their current range. The increase was in great part due to the estimated  
 308 increase in selection for high-elevation areas that are well outside the population's current  
 309 range.

## 310 4 Discussion

311 We have demonstrated that temperature is an important determinant of whether, how, and  
 312 where mammals move, even while accounting for seasonality (e.g., changes in photoperiod,  
 313 hormones, and resources). Disentangling temperature from other drivers is important for  
 314 predicting how changes in climate will affect mammalian movement when other drivers re-  
 315 main approximately constant. However, predicting mammals' responses to climate change



**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 ( $\approx 2^{0.585}$ ; 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.

becomes increasingly complex as habitats warm and animals are exposed to increasingly frequent conditions that are both extreme and novel. Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 2 and 3 comes with substantial uncertainty, particularly given that the responses are nonlinear. At unusually warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020; Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators, and/or prey can often be substantially different from the behaviour at typical temperatures. As extreme temperature events become more frequent and prolonged (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical behaviours that may alter community structures and behaviours, both during such events and afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance, changes in climate and phenology impact the life history and behaviour of many hibernating mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021). Such changes may alter the frequency and intensity of human-wildlife conflict, especially with the addition of growing pressures from human development and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*, 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being predated upon (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022; Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009; Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences for population and ecosystem structures and dynamics as prey, predators, and competitors experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et al.*, 2011).

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, typ-

ical 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. Additionally, communicating uncertainty in one's estimates is crucial in assessing risk probabilistically (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann, 2014). Recent events in global politics, including global conflicts (McNutt & Hildebrand, 2022; Tollefson, 2022) and the rapid rise in generative machine learning (more commonly: "AI," see Roumeliotis & Tselikas, 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*, 2025) and its prohibitive energy and water demands (Li *et al.*, 2023) and carbon footprint (Luccioni *et al.*, 2024), have placed doubt on the feasibility of reaching climate change goals that seemed achievable in the past decade (United Nations Environment Programme *et al.*, 2024). Mitigating climate change and its consequences will require extensive and widespread collaborative effort (Huang & Zhai, 2021). Similarly, protecting a third of the world's ecosystems (Section H, Targets 2 and 3 of Convention on Biological Diversity, 2022) appears less tangible as global political and environmental conditions change rapidly and unpredictably (Sih *et al.*, 2011; Simmons *et al.*, 2021; Guenette *et al.*, 2022; Sovacool *et al.*, 2023). Achieving the "30 by 30" goal will require active partnership with local Peoples, especially Indigenous Peoples (Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences of climate change on mammals' movement behaviour and spatial distribution is a first step towards anticipating and proactively responding to future changes in human-induced rapid environmental change (Sih *et al.*, 2011; Williams & Blois, 2018). In the following sections, we discuss the implications of our results in more detail. We then expand on consequences for conservation during the 21<sup>st</sup> century and considerations for future studies.

368 **4.1 Effects of temperature on movement rates**

369 The lack of common effects of temperature across all species' movement rates indicates that  
370 preparing for future changes will require a variety of physiological and behavioral adaptations  
371 as ecological communities respond in complex and interconnected ways. Although our models  
372 do not account for explicit physiological or phenological changes, the tensor product terms  
373 in Fig. 2 suggest that warmer temperatures cause many species to alter their daily and  
374 seasonal activity patterns (most visible in pumas and grizzly bears). For example, when  
375 temperatures were above 0°C, pumas moved most at night, but when temperatures were  
376 below 0°C they tended to move more throughout the day. Throughout the year, they adapted  
377 their tolerance to temperature and moved less when it was relatively hot (for a given time  
378 of year), especially in spring and summer. The strong reduction in the mid-day movement  
379 rates of wolves, elk, pumas, and boreal caribou when summer temperatures were above  
380 20°C suggests that the increasingly common and intense heat waves across British Columbia  
381 will have community-wide impacts on movement rates, encounter rates, and potentially  
382 community structure (Martinez-Garcia *et al.*, 2020). More work is necessary on quantifying  
383 interspecific responses to temperature, including the effects of temperature on predation  
384 rates (but see: Cunningham *et al.*, 2021; Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase  
385 in intensity and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022)  
386 will likely also impact the occurrence and timing of hibernation (Wells *et al.*, 2022) and  
387 migration or seasonal range expansions (Morley, 2021; Carbeck *et al.*, 2022; Malpeli, 2022).  
388 However, not all species may be able to adapt at the current rate of climate change (Heten  
389 *et al.*, 2014; Williams & Blois, 2018), especially since landscape changes will likely depend  
390 not only on the direct effect of temperature but also on cascading changes in the availability  
391 and unpredictability of resources (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Mezzini  
392 *et al.*, 2025).

393 **4.2 Effects of temperature on habitat selection**

394 As with the effects of temperature on movement rates, the lack of common effects of  
395 temperature across all species indicates that efficient and proactive habitat conservation  
396 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
397 physiological responses to temperature that may impact movement, such as changes in the  
398 phenology of plants, ice, or mammalian physiology or behaviour (e.g., moulting, migration),  
399 other than as direct responses to temperature. Consequently, the behavioural changes we  
400 present should be interpreted carefully. While some seasonal cycles do not depend directly  
401 on temperature and may thus not be impacted directly by climate change (such as those  
402 driven by photoperiod, see Liu *et al.*, 2022), the predictions we present also rely on the  
403 assumption that mammals will not adapt these seasonal cycles to temperature-dependent  
404 cues, such as weather (Xu & Si, 2019) or forage availability (Middleton *et al.*, 2018), which  
405 may not be correct. Additionally, it is important to stress the distinction between habitat  
406 selection and quality. While animals tend to select for high-quality habitats (Kacelnik *et al.*,  
407 1992; Wright, 2024), high selection strength can also be a consequence of an ecological trap  
408 (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*, 2021).

409 **4.3 Predicted changes in movement during the 21<sup>st</sup> century**

410 Achieving the goals laid out by the “30 by 30” conservation initiative (Section H, Targets 2  
411 and 3 of Convention on Biological Diversity, 2022) will require careful planning but often also  
412 rapid action. In the case of Canada, only 13.7% of its terrestrial areas and inland waters were  
413 protected at the end of 2023 (Environment and Climate Change Canada, 2024; Minister of  
414 Environment and Climate Change, 2024). Additionally, efficient and effective conservation  
415 will require collaboration with Indigenous and local communities to ensure Treaties are  
416 respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020; e.g., Falardeau *et al.*,  
417 2022; Lamb *et al.*, 2023) while also actively preparing for future change (Desjardins *et al.*,  
418 2020; Hessami *et al.*, 2021). The large range in predicted changes by 2100 (both across

species and within species' current ranges) and high spatial heterogeneity in Fig. 7 highlight the need for careful planning that incorporates not only reliable estimates of change but also pragmatic and communicable measures of uncertainty and variability around such estimates. The width of the prediction intervals in Fig. 4 suggest that spatial and intra-individual variation should be accounted for when deciding the location and size of protected areas. Accurate estimates of the effects of changes in temperature on mammals' movement require a holistic view of the direct effects of temperature on mammals' movement directly as well as its effects on other drivers of movement, such as forage and prey availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*, 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*, 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation among the responses of different species (and individuals), especially as populations a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and likely decreases), some animals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*, 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

#### 4.4 Considerations for future studies

Our work highlights three central considerations for future research: (1) telemetry sampling rates should be designed primarily in relation to the movement timescales of the species of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of individuals tracked and the length of each telemetry should depend not just on population size but also environmental stability, and (3) predicting changes in movement behaviour becomes highly complex when responses are nonlinear, especially when changes depend on

445 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses  
446 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020). We  
447 address each consideration in the following three paragraphs.

448 While the `ctmm` models produced scale-independent estimates of speed (i.e., model inter-  
449 pretation is independent of sampling interval: Noonan *et al.*, 2019a), the accuracy, size, and  
450 stability of speed estimates still depended on the GPS sampling frequency. This is because  
451 coarsely-sampled movement data contains information on large-scale movements (e.g., range  
452 crossings, migrations) but not fine-scale movements (e.g., first-order habitat selection *sensu*  
453 Johnson, 1980; also see Nathan *et al.*, 2022). Using the boreal caribou as an example, the  
454 13-hour sampling interval allows us to reasonably estimate the caribou's movement path at  
455 a temporal scale of approximately 13 hours (or greater), but we cannot produce reasonable  
456 movement trajectories at a much finer (e.g., hourly) scale. Consequently, we suggest being  
457 cautious when comparing estimated movement behaviours across species, even though all  
458 predictions have been corrected to the hourly timescale by predicting for 1-hour time inter-  
459 vals (i.e., `dt_hours = 1`). Thus, sampling schedules should be fine enough to reconstruct  
460 animals' movement at a sufficiently fine scale. Good estimates of an animal's speed and its  
461 movement path require telemetry locations to be taken more often than the animal's direc-  
462 tional persistence (Noonan *et al.*, 2019a), so that, on average, the dataset contains multiple  
463 locations in between changes in direction. What constitutes a change in direction depends  
464 on what movement scale one is investigating. Small-scale movements and first-order spa-  
465 tial selection will require more frequent sampling than migratory movement or second- and  
466 third-order spatial selection. While `ctmm` movement models are scale-invariant in that any  
467 model can be scaled to larger or smaller areas and timescales, the model estimates are not  
468 independent of the scale of the sampling frequency.

469 When landscapes are relatively predictable across years, a larger number of sampled in-  
470 dividuals is likely preferable over longer, multi-year telemtries. This allows one to quantify  
471 the variance across individuals, including the range of conditions and environments that indi-

472 vidual animals are in. A good estimate of inter-individual variance provides better coefficient  
473 estimates along with more appropriate measures of uncertainty. However, when conditions  
474 across years are relatively stochastic, multi-year telemetries allow one to better estimate  
475 inter-annual variation without conflating it with inter-individual differences. In either case,  
476 carefully-designed sampling schedules and (Bayesian) hierarchical models can provide good  
477 estimates of the effects of interested along with appropriate measures of uncertainty (Czado  
478 & Brechmann, 2014; McElreath, 2020).

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

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