

The heat is on: Rising temperatures alter when, how, and where  
large terrestrial mammals move

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## Abstract

Widespread warming during the last century 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 quantitatively estimated the effects of temperature on mammalian movement behaviour, but few have estimated the effects of future climate change. Consequently, it is still unclear how mammals will adapt their movement behavior 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 western Canada between 1998 and 2023. We show that temperature is a strong determinant of when, how, and where mammals move, and we predict that climate change will impact mammals' movement rates and habitat selection as temperatures warm throughout the 21<sup>st</sup> century. We found the effects of temperature on movement rates varied across species, so we suggest that species' estimated responses be interpreted holistically when making inferences about how climate change will impact ecological communities. In contrast, habitat selection strength decreased for all species within their observed ranges, suggesting that all six species may 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, with particular attention to the study design, statistical modeling, and forecasting.

<sup>1</sup> **1 other refs**

- <sup>2</sup> • Gerlich *et al.* (2025): effects of temperature on fly movement in the arctic
- <sup>3</sup> • “Potential changes in climate indices in Alberta under projected global warming of
- <sup>4</sup>    1.5–5 °C” (<https://www.sciencedirect.com/science/article/pii/S2214581823000770#fig0015>)
- <sup>5</sup> • Global vulnerability of marine mammals to global warming: <https://doi.org/10.1038/s41598-019-57280-3>
- <sup>6</sup> • marine turtles shift and lose habitat with temperature: <https://www.science.org/doi/10.1126/sciadv.adw4495>
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<sup>10</sup> **2 Introduction**

<sup>11</sup> For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan  
<sup>12</sup> *et al.*, 2008). Animals move to maximize resource availability (e.g., food, water, shelter;  
<sup>13</sup> Charnov, 1976; Kacelnik *et al.*, 1992), optimize habitat use (Winter *et al.*, 2024), and escape  
<sup>14</sup> predation (Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). However,  
<sup>15</sup> ambient temperature affects mammals' movement rates by altering the energetic cost of  
<sup>16</sup> movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn &  
<sup>17</sup> Seebacher, 2022) and the risk of overheating (Heten *et al.*, 2014; Dyer *et al.*, 2023). Animals  
<sup>18</sup> may search for a short-term buffer from extreme heat or cold via thermal refugia (Hannah  
<sup>19</sup> *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland  
<sup>20</sup> *et al.*, 2022), which may even be preferred over forage abundance (e.g., Hall *et al.*, 2016).

<sup>21</sup> Temperature also has indirect effects on movement through other drivers of movement  
<sup>22</sup> behaviour, such as trophic interactions (Hegel *et al.*, 2010), snow depth and density (Mont-  
<sup>23</sup> gomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), altered phenology [Bunnell *et*  
<sup>24</sup> *al.* (2011); ], and the frequency and intensity of extreme events (Bunnell *et al.*, 2011; Zhang  
<sup>25</sup> *et al.*, 2023), including forest fires, droughts, and extreme weather (Bunnell *et al.*, 2011;  
<sup>26</sup> Duncan *et al.*, 2012; Merkle *et al.*, 2016; Berger *et al.*, 2018; Slatyer *et al.*, 2022; Zurowski,  
<sup>27</sup> 2023). Changes in temperature thus affect how animals move (e.g., movement frequency and  
<sup>28</sup> speed – their movement behaviour: Nathan *et al.*, 2008; Dyer *et al.*, 2023) and where they  
<sup>29</sup> move to (i.e., their habitat selection: Merkle *et al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*,  
<sup>30</sup> 2023).

<sup>31</sup> By impacting animal movement behavior, temperature also affects the consequences of  
<sup>32</sup> movement, such as encounter rates with resources (Mezzini *et al.*, 2025), other animals  
<sup>33</sup> (Martinez-Garcia *et al.*, 2020), and humans (Weststrate *et al.*, 2024), and these changes are  
<sup>34</sup> exacerbated at extreme temperatures (Wilson *et al.*, 2001; Berger *et al.*, 2018; Giroux *et al.*,  
<sup>35</sup> 2023). But what counts as “extreme” varies across species: Species that experience narrow

36 temperature ranges tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga*  
37 *tridactyla*: Giroux *et al.*, 2023), while thermal generalists can adapt more easily to change  
38 (Levins, 1974; Botero *et al.*, 2015; Dupont *et al.*, 2024). However, generalists' greater  
39 adaptability is tested when they are subject to changes that are more severe (McCain, 2019),  
40 affect many factors (e.g., temperature, phenology, and resource availability: Polazzo *et al.*,  
41 2024), or are too rapid to respond within the span of a lifetime or a few generations (Levins,  
42 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

43 In the last 200 years, many ecosystems experienced widespread warming that resulted  
44 in milder and shorter winters, hotter and longer summers, and a greater risk of extremely  
45 high temperatures (IPCC, 2023). Over the next 100 years, these changes are expected to  
46 worsen and continue to impact mammals' fitness, movement behaviour, and habitat selec-  
47 tion as animals cope with growing heat stress (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020)  
48 and more frequent and intense extreme events (Bunnell *et al.*, 2011), along with increas-  
49 ing anthropogenic pressure (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024).  
50 Consequently, it remains unclear how or whether species will be able to respond to climate  
51 change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*,  
52 2023), especially when populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et*  
53 *al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams &  
54 Blois, 2018). Uncertainty in future conditions and their consequences on ecosystems present  
55 a need for a comprehensive understanding of (1) the direct effects of temperature on animal  
56 movement behaviour and (2) the implications such changes and uncertainty will have on  
57 populations and species' adaptability and resiliency, as well as overall community structure.  
58 Recent work has documented the effects of climate change on mammals' ranges (Leclerc *et*  
59 *al.*, 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*,  
60 2021), and trait-based responses (e.g., body size, activity time, and elevational and lati-  
61 tudinal distribution McCain, 2019). However, it is still unclear how mammals will adapt  
62 their small-scale movement and habitat selection to changes in temperature during the 21<sup>st</sup>

63 century (IPCC, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024).

64 Understanding the direct and indirect impacts of temperature on mammalian movement  
65 is essential for decision makers to respond to change in a proactive manner (Sawyer *et al.*,  
66 2009; McCain, 2019). Western Canada is currently experiencing rapid widespread warming  
67 (Turner & Clifton, 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle,  
68 2018; Basu *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang  
69 *et al.*, 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the  
70 “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands and  
71 oceans by 2030 (Convention on Biological Diversity, 2022), decision makers must understand  
72 which areas will be of greatest value for maximizing the project’s effectiveness. Predicting  
73 how climate change will affect how, when, and where animals will move is necessary for  
74 identifying landscape dynamics and value will evolve throughout the century. Failing to  
75 understand how changes in temperature will affect mammalian movement behaviour and  
76 habitat selection will hinder our ability to respond to the current climate crisis and make  
77 decisions that are viable in the long term.

78 This paper provides a framework for quantifying the effects of proximal air temperature  
79 on animal movement using quantitative methods that are flexible and statistically robust.  
80 We present results for six large-bodied terrestrial mammal species in western Canada (wolves:  
81 *Canis lupus*, elk: *Cervus canadensis*, mountain goats: *Oreamnos americanus*, cougars: *Puma*  
82 *concolor*, boreal and southern mountain caribou: *Rangifer tarandus*, and grizzly bears: *Urs-*  
83 *sus arctos horribilis*; Table 1). Using over 25 years of telemetry data throughout a large  
84 spatial range of western Canada and hourly air temperature data, we estimate how these  
85 mammals altered their probability of movement, speed when moving, and habitat selec-  
86 tion in response to temperature. We then pair the estimated responses with climate change  
87 projections to forecast the species’ movement during the 21<sup>st</sup> century under different climate-  
88 change scenarios (referred to as Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017).  
89 We disentangle the direct and indirect effects of temperature on the movement behaviour

90 of terrestrial mammals and discuss the consequences of these changes at the individual,  
 91 population, and community levels.

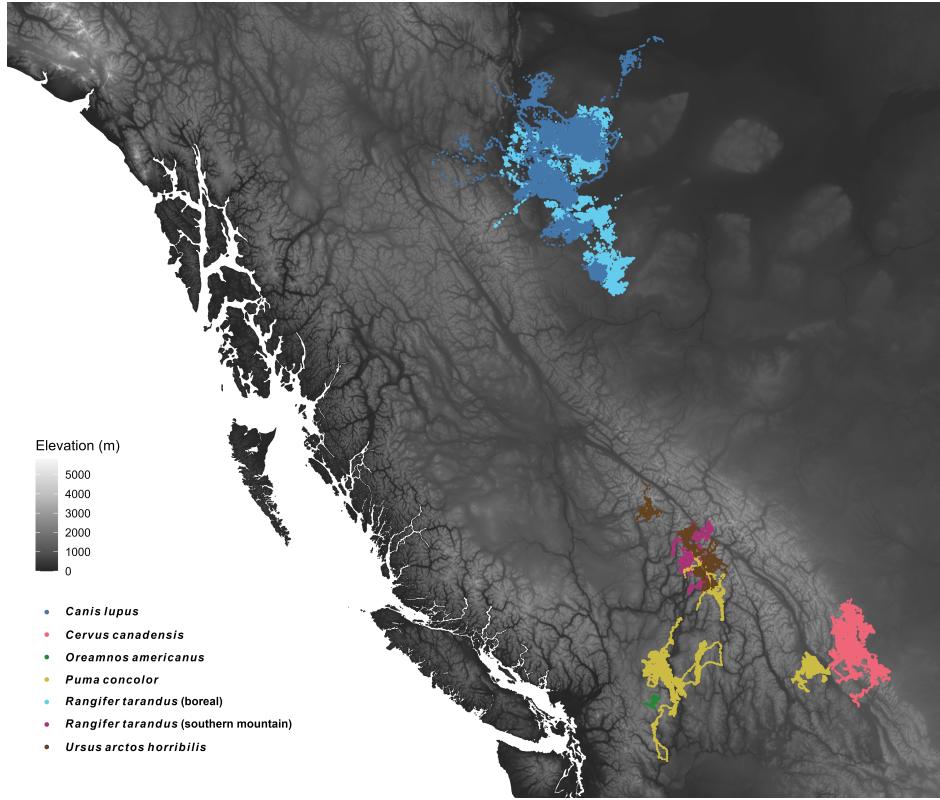


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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

92 **3 Methods**

93 **3.1 Datasets used**

94 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry  
95 data (Fig. 1); (2) historical hourly reanalyzed air temperature from the ERA5 dataset from  
96 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent  
97 forest cover, elevation, and distance from water; and (4) climate change projections under  
98 four Shared Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). While we acknowledge  
99 that forest type, structure, and age are important variables, we do not include such variables  
100 in this study for the sake of parsimony and comparability across species. We detail the data  
101 sources and analyses in the sections below.

102 **3.1.1 GPS telemetry data**

103 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
104 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou  
105 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public British  
106 Columbia Oil and Gas Research and Innovation Society repository (<https://www.bcgiris.ca/projects/boreal-caribou-telemetry-data>). **MISSING INFO ON OTHER TELEME-**  
107 **TRY DATA.** From the full set of telemetry data, a total of 2396 GPS locations (0.16%,  
108 including collar calibration data) were removed using diagnostic plots of (1) distance from  
109 the median location, (2) straight-line displacement between locations, (3) turning angle, and  
110 (4) time interval between consecutive points. Particular attention was paid to points with  
111 large turning angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially if  
112 antecedent and subsequent points indicated stationary behaviour (Appendix A).

114 **3.1.2 Historical temperature data and temperature projections**

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

121 We obtained rasters of projected monthly average temperature for the study region at a  
122 0.08° spatial resolution from 2020 to 2100 under the different SSPs via the `climatenetR` pack-  
123 age (version 1.0, Burnett, 2023) for R. Since the climate projections only provided monthly  
124 means and ranges but no measures of variance or distributional assumptions, we used the  
125 hourly ERA5 reanalyzed data for western Canada from 1998 to 2023 (extremes included,  
126 Hersbach *et al.*, 2023) to calculate within-month variance in temperature, which we defined as  
127 the variance within a given pixel, month, and year. We then modeled the estimated variance  
128 using a GAM for location and scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos &  
129 Rigby, 2007; section 7.9 in Wood, 2017). The linear predictor for the location (i.e., the mean)  
130 included smooth terms of the within-pixel monthly mean temperature (within each year),  
131 month (as a cyclic smooth), a two-dimensional smooth of space, and a tensor interaction  
132 product term of space and month. The linear predictor for the scale term (which governs the  
133 mean-variance relationship) included smooth terms of the monthly mean, month, and space.  
134 We did not include a smooth of year to avoid unrealistic projections when extrapolating  
135 beyond the range of historical data.

136 We simulated hourly variation in future weather by assuming hourly temperature fol-  
137 lowed a normal distribution with mean specified by the monthly `climatenetR` climate pro-  
138 jections and variance as specified by the Gamma GAMLS. For each month within each year  
139 from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to  
140 the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the

141 (normalized) Gaussian probability density for each quantile.

### 142 3.1.3 Resource rasters

143 We estimated percent forest cover and distance from water using the rasters created by  
144 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
145 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
146 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
147 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover  
148 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the  
149 nearest pixel with water using the `distance()` function from the `terra` package. Finally,  
150 we obtained two digital elevation models using the `get_elev_raster()` function from the  
151 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom  
152 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate  
153 change projections via `climatenar`. All final rasters and code are available on GitHub at  
154 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

## 155 3.2 Estimating mammals' instantaneous speeds

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

163 Since ‘`ctmm`’s movement models assume stochastic but non-zero speeds (i.e., a sin-  
164 gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
165 minimum instantaneous speed could be 0. We performed this correction by subtracting

166 each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
167 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  
168 small, non-zero speeds, we determined whether an animal was moving or not using a  $k$ -means  
169 algorithm with 2 clusters for each species' detrended speeds. When the algorithm clearly  
170 failed to discriminate between states, we estimated the split point using the inflection points  
171 in histograms of the detrended speeds (Fig. B1).  
172

### 173 3.3 Estimating the effects of temperature on mammals' movement

174 The following sections detail the statistical framework and modelling we used to estimate  
175 the effect on temperature on mammals' movement. To assess the importance of including  
176 temperature as an explicit covariate (rather than including its effects with time of day and  
177 day of year), we fit models with and without smooth effects of temperature and compared  
178 the fits of the two sets of models.

#### 179 3.3.1 Disentangling direct and indirect effects

180 In this study, we separate the effects of temperature on mammalian movement into direct  
181 and indirect effects. We call "direct" all effects that impact movement behavior causally  
182 without first impacting another variable (Fig. 2). For example, in Fig. 2A, whether a  
183 grizzly bear is moving in a given moment directly depends on time of day and day of year,  
184 since it will not be moving when sleeping or hibernating. However, time of day and day of  
185 year also impact its movement behavior indirectly because its sensitivity to temperature will  
186 also depend on time of day and day of year. Thus, both time of day and day of year also  
187 impact movement frequency indirectly by altering the effect of temperature on movement  
188 frequency. Failing to disentangle the effects of these three variables will lead to incorrect and  
189 likely confusing estimates for the causal effect of temperature on movement behavior, since  
190 causal and non-causal relationships would be indistinguishable (McElreath, 2020).

191 Indirect effects of temperature also include all effects that can be controlled by altering  
 192 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022). For example, in Fig.  
 193 2B, an increase in temperature may push an animal to prefer higher forest cover in search of  
 194 shade, and conservationists can mitigate these indirect effects of temperature by increasing  
 195 the availability of forested areas, since the effect of temperature on movement is conditional  
 196 on forest cover availability. In contrast, the animal may avoid moving if temperatures are  
 197 above 35°C, irrespective of its geographic and environmental space (*sensu* Matthiopoulos,  
 198 2022). In this case, it is not possible to mitigate the effects of temperature on movement  
 199 behaviour (other than changing temperature directly).

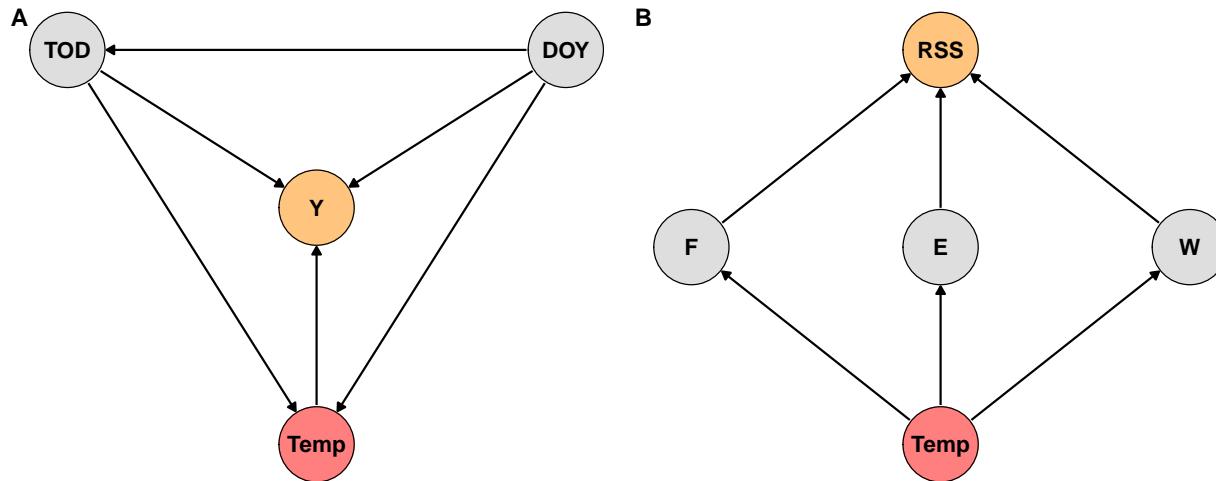


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled (Y) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction effects. Temperature directly affects Y, but the effects of temperature depend on the time of day and season. Time of day and day of year also affect Y directly, but the effect of time of day changes throughout the year due to changes in day length and seasonality. (B) DAG for Relative Selection Strength (RSS) for percent forest cover (F), elevation (E), and distance from water (W). The RSS for of a given habitat depends on all three resources, and the selection for each resource is independent of the other two resources and dependent on temperature.

### 200 3.3.2 Effects of temperature on movement rates

201 We estimated the effects of temperature (°C) on mammals' instantaneous movement state  
 202 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models  
 203 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R  
 204 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was  
 205 moving,  $P(M)$ , with a binomial family of distributions and logit link function. The response

206 variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an  
207 animal's speed when moving (`speed`) with a gamma family of distributions and log link  
208 function.

209 The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`),  
210 fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(...,`  
211 `by = species)`), which allowed each species' term to be estimated independent of other  
212 species (see model I in Figure 4 of Pedersen *et al.*, 2019). The `by` smooths accounted for  
213 trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and tempera-  
214 ture (`temp_c`). The models also had three tensor product interaction terms (`ti()`) by each  
215 species: (1) day of year and time of day, (2) temperature and time of day, and (3) tempera-  
216 ture and day of year. These three terms accounted for: (1) seasonal changes in day length,  
217 (2) hourly changes in the response to temperature (e.g., changes in nocturnality), and (3)  
218 seasonal changes in the response to temperature (e.g., changes in coats and migration tim-  
219 ing). Finally, smooth terms of log-transformed hours between GPS locations (`dt`) accounted  
220 for irregular sampling rates. A global term of `log(dt)` accounted for the overall effect  
221 of sampling interval, while a factor-smooth interaction term (`s(log(dt), species, bs =`  
222 `'fs')` allowed for species-level deviations from the global term while assuming a common  
223 smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).

224 The HGAMs accounted for the cyclicity of time of day and day of year using cyclic  
225 cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). We fit the models with fast Restricted  
226 Maximum Likelihood ('`fREML`') and discretized covariates (`discrete = TRUE`) to optimize  
227 computational efficiency with no appreciable losses to model performance (Appendix B;  
228 Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma  
229 HGAM inform us on an animal's long-term average speed, since it is the product of the  
230 probability of moving and its average speed when moving.

```

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)))

```

231 3.3.3 Effects of temperature on habitat selection

232 We estimated the effects of temperature on each species' selection for percent forest cover  
 233 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 234 ting a Hierarchical Resource Selection Function for each species using an HGAM with a  
 235 Poisson family of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After  
 236 removing non-resident individuals (Table B1), we accounted for the spatiotemporal auto-  
 237 correlation in the telemetry locations by weighting each point based on the telemetry's  
 238 Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b)  
 239 to produce estimates of second- and third-order habitat selection (Johnson, 1980). While  
 240 we recognize there are other important drivers of habitat selection (e.g., forest age, forest  
 241 type, terrain ruggedness, prey availability), we decided to only use these three proxies to  
 242 produce results that are easily comparable across species. Each species' model had the same

243 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)
```

244 Smooth effects of percent forest cover, elevation, and distance to water accounted for  
245 the species-level average selection strength for each resource. A random effect for each in-  
246 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
247 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
248 selection (i.e., individual-level deviations from the species-level average; Jeltsch *et al.*, 2025).  
249 Tensor interaction product terms (`ti()`) of the three resources and temperature estimated  
250 the change in resource selection at different temperatures. Finally, we included marginal  
251 smooth terms of temperature to account for species- and individual-level sampling biases  
252 over temperature (e.g., sampling more during warm periods). Detections were weighted  
253 proportionally to their degree of independence from other temporally proximate detections  
254 (`weights = weight` – Appendix B; Alston *et al.*, 2022), while quadrature points had a weight  
255 of 1. Quadrature points were obtained using all raster cells in the 99.9% AKDE percentile.  
256 The number of quadrature locations greatly outnumbered the number of observed locations  
257 (Fig. B12), especially after accounting for weighting based on the degree of autocorrelation  
258 and the number of home range crossings (Fig. B13).

259 **4 Results**

260 Overall, 2.6% of GPS locations had temperatures lower than  $-20^{\circ}\text{C}$ , while 6.5% had temper-  
261 atures above  $20^{\circ}\text{C}$ , and temperature ranges differed across species (Table 2, Fig. B2). At  $0^{\circ}\text{C}$ ,  
262 species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed  
263 when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e.,  $P(M) \times \mathbb{E}(S)$ ,  
264 range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ( $P(M) \approx 0.05$ ),  
265 while wolves and cougars moved most often ( $P(M) \geq 0.22$ ). When moving, mountain goats  
266 and southern mountain caribou moved the slowest ( $\mathbb{E}(S|M) \approx 0.43$  km/h), while wolves  
267 had the highest mean speed when moving ( $\mathbb{E}(S|M) \approx 2.64$  km/h). Consequently, wolves  
268 traveled, on average, 0.6 km/h – 2.5 to 16.7 times further than other mammals at  $0^{\circ}\text{C}$ .

Table 2: Percentage of observed GPS locations (after data cleaning) with temperatures below  $-20^{\circ}\text{C}$  or above  $20^{\circ}\text{C}$ .

Species	T < $-20^{\circ}\text{C}$	T > $+20^{\circ}\text{C}$
Canis lupus	1.7 %	13.0 %
Cervus canadensis	2.4 %	4.9 %
Oreamnos americanus	0.7 %	2.8 %
Puma concolor	0.7 %	6.9 %
Rangifer tarandus (boreal)	6.8 %	7.9 %
Rangifer tarandus (s. mountain)	1.3 %	3.4 %
Ursus arctos horribilis	0.0 %	8.4 %
Total	2.6 %	6.5 %

Table 3: Mean probability of movement ( $P(M)$ ), speed ( $\mathbb{E}(S)$ , km/h, assuming constant movement), and distance travelled ( $P(M) \times \mathbb{E}(S) = \mathbb{E}(D)$ , km/h) 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

Near  $0^\circ\text{C}$ , wolves selected for dense forest cover ( $\gtrapprox 50\%$ ), elevations near 1 km, and distances from water  $< 10$  km; elk selected for forest cover near 50%, elevations between 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (< 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover, an elevation of  $\sim 1$  km, and distances from water  $< 10$  km; boreal caribou selected for intermediate to dense forest cover, elevations near 500 m, and distances from water  $< 10$  km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances from water  $< 5$  km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances from water  $< 2$  km.

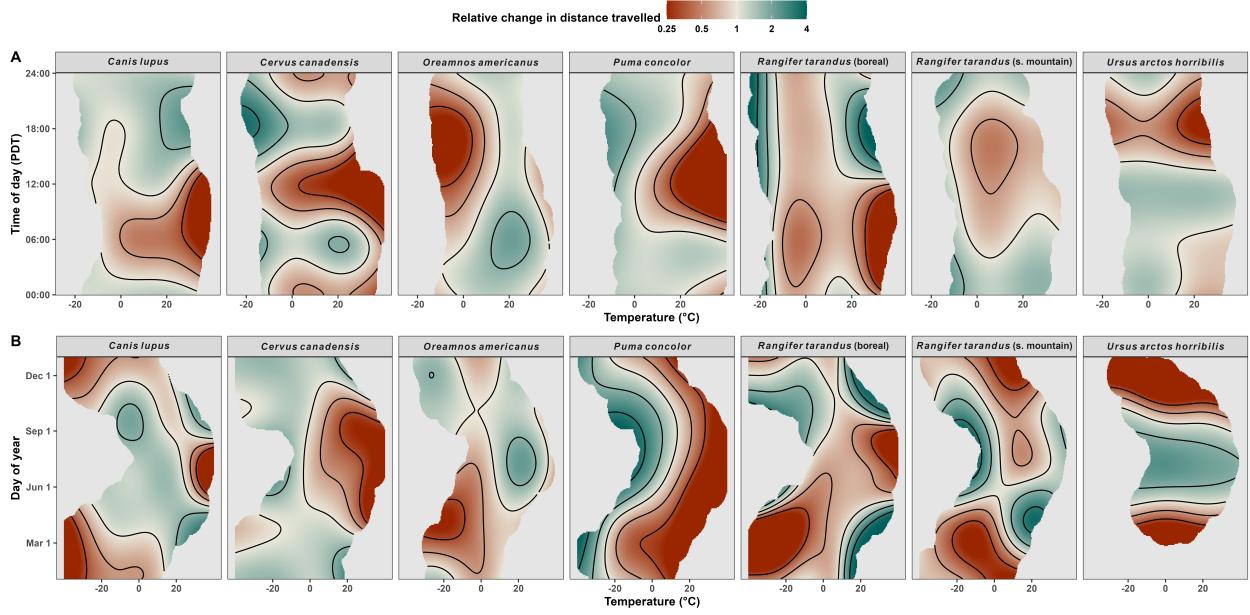
There was relatively strong agreement between models with and without temperature (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses of deviance showed that temperature significantly affected movement behavior (all p-values  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \geq 342$ ; Table B2 and following pages in Appendix B). Accounting for temperature resulted in a simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better (lower deviance), and hence no test was necessary to show that the inclusion of temperature produced a better fit.

285 **4.1 Effects of temperature on movement rates**

286 The effects of temperature on movement rates varied in both direction and magnitude across  
287 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
288 migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and  
289 indicated clear shifts in activity over time of day and day of year for all species. The  
290 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions  
291 of the deviance (79.3% for the Gamma model and 10.7% for the binomial model, which is  
292 relatively high for a binomial model with binary responses: see ch. 11 of McElreath (2020)].  
293 All species adapted their daily and seasonal movement behaviour to changes in temperature  
294 (Fig. 3). The clearest example of this was cougars. In mid summer, they moved mostly  
295 in the evening if temperatures were cool and mostly in the early morning if temperatures  
296 were hot. Throughout the year, they tended to move more when it was colder, but what  
297 they perceived as “colder” depended on the time of year. However, uncertainties around  
298 the estimated effects were often higher at extreme temperatures due to data scarcity. All  
299 species’ estimated probability of moving decreased with sampling intervals approximately  
300 above 1 hour, and most species’ estimated speed when moving decreased monotonically with  
301 sampling interval, although the estimated trends were highly uncertain for some species (Fig.  
302 B8).

303 **4.2 Effects of temperature on habitat selection**

304 Species’ relative selection strength (RSS) was generally strongest for elevation and weak-  
305 est for forest cover, but species’ RSS for resources depended on temperature (Fig. 4).  
306 Changes in RSS with temperature were also strongest for elevation and generally weak-  
307 est distance from water, but there were no common trends across all species for any of the  
308 three resources. All species, with the exception of cougars, exhibited a clear temperature-  
309 dependent shift in their preference for forest cover. At higher temperatures, wolves, mountain  
310 goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted



**Figure 3: 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.

311 towards more intermediate forest cover without much of a change in preference width. All  
312 species shifted elevationally with temperature, although boreal caribou's selection strength  
313 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain  
314 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,  
315 and grizzly bears decreased in elevation. Most species generally remained within 5 km of  
316 water, and temperature did not affect their selection strength as much as for the other two  
317 resources. Again, estimated RSS values were generally most uncertain at extreme tempera-  
318 tures (Fig. B15).

### 319 4.3 Predicted changes in movement during the 21<sup>st</sup> century

320 The predicted changes in distance traveled varied across species in both direction and magni-  
321 tude, but worse climate-change SSPs always corresponded to greater absolute changes (Fig.  
322 5). Additionally, species that were predicted to move less often did not necessarily have lower  
323 speeds when moving, and vice versa (Figs. B9 and B10). Overall, absolute changes by 2100  
324 under the best-case SSP were small (approximately 0% to +4%), while under the worst-case

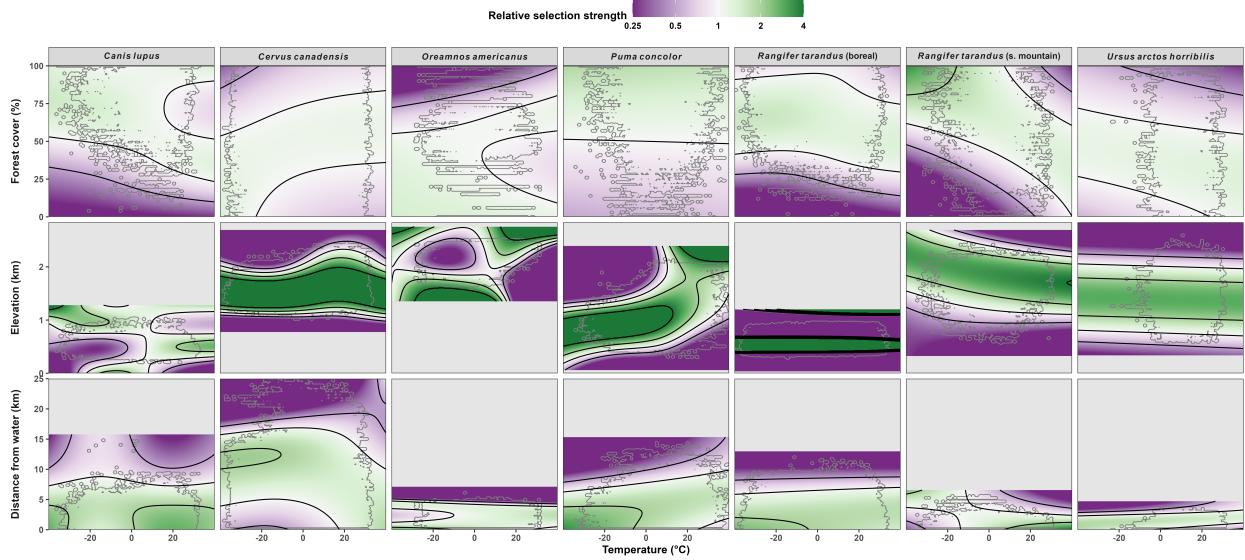


Figure 4: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered and capped to  $2^{\pm 2}$  to improve readability.

325 SSP absolute changes ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while  
 326 the models estimated that grizzly bears would move substantially less (if at all) in winter  
 327 (Figs. 3, B4-B6), the models did not explicitly account for changes in hibernation phenol-  
 328 ogy. Consequently, the climate change projections do not explicitly account for changes in  
 329 energetic needs or physiology. Projected changes also varied spatially due to heterogeneity  
 330 in projected climate change (Fig. 6). Again, absolute changes were generally greatest under  
 331 worse SSPs, but the direction of change at each location also varied across SSPs (most visible  
 332 in cougars).

333 Median RSS was projected to decrease over time within the each species' observed range,  
 334 but changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced in  
 335 the bottom fifth percentile and most severe for elk, southern mountain caribou, and mountain  
 336 goats. Of all the species, only cougars showed a clear increase in RSS for areas within their  
 337 current range. The change in RSS between 2025 and 2100 varied spatially for all species  
 338 (Fig. 8). All species were predicted to exhibit a decrease in RSS throughout most of their  
 339 observed habitats, although cougars were predicted to increase their selection for patches  
 340 with higher altitude.

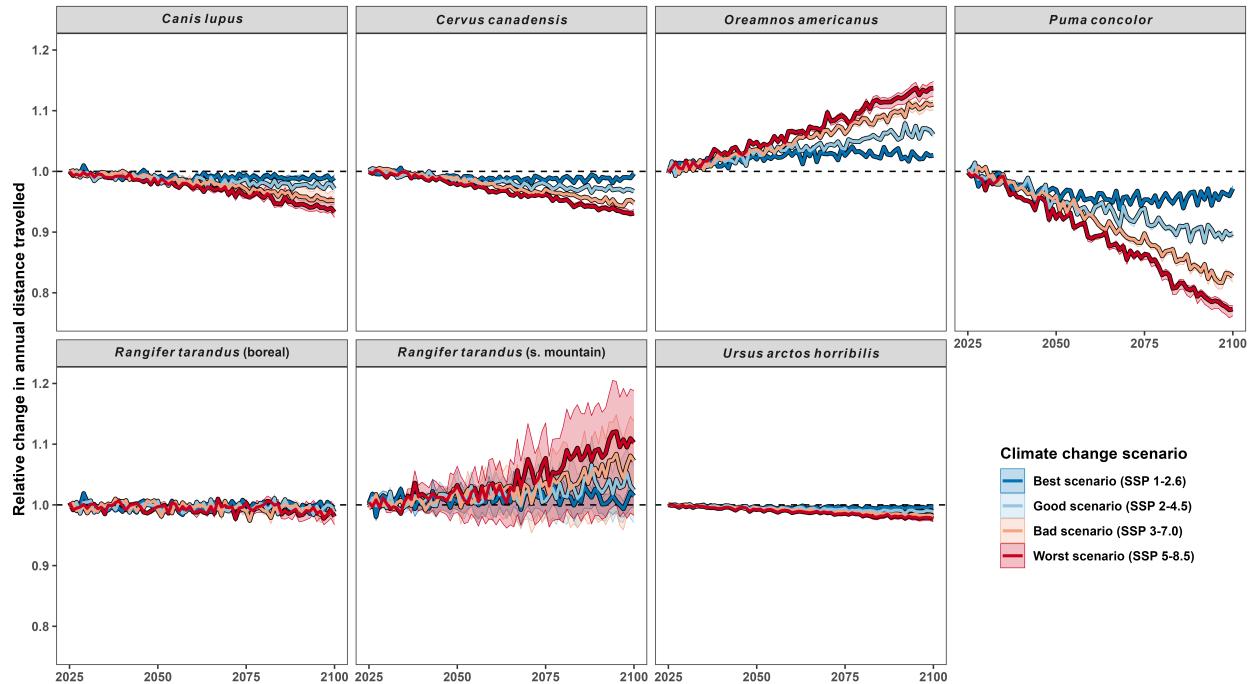
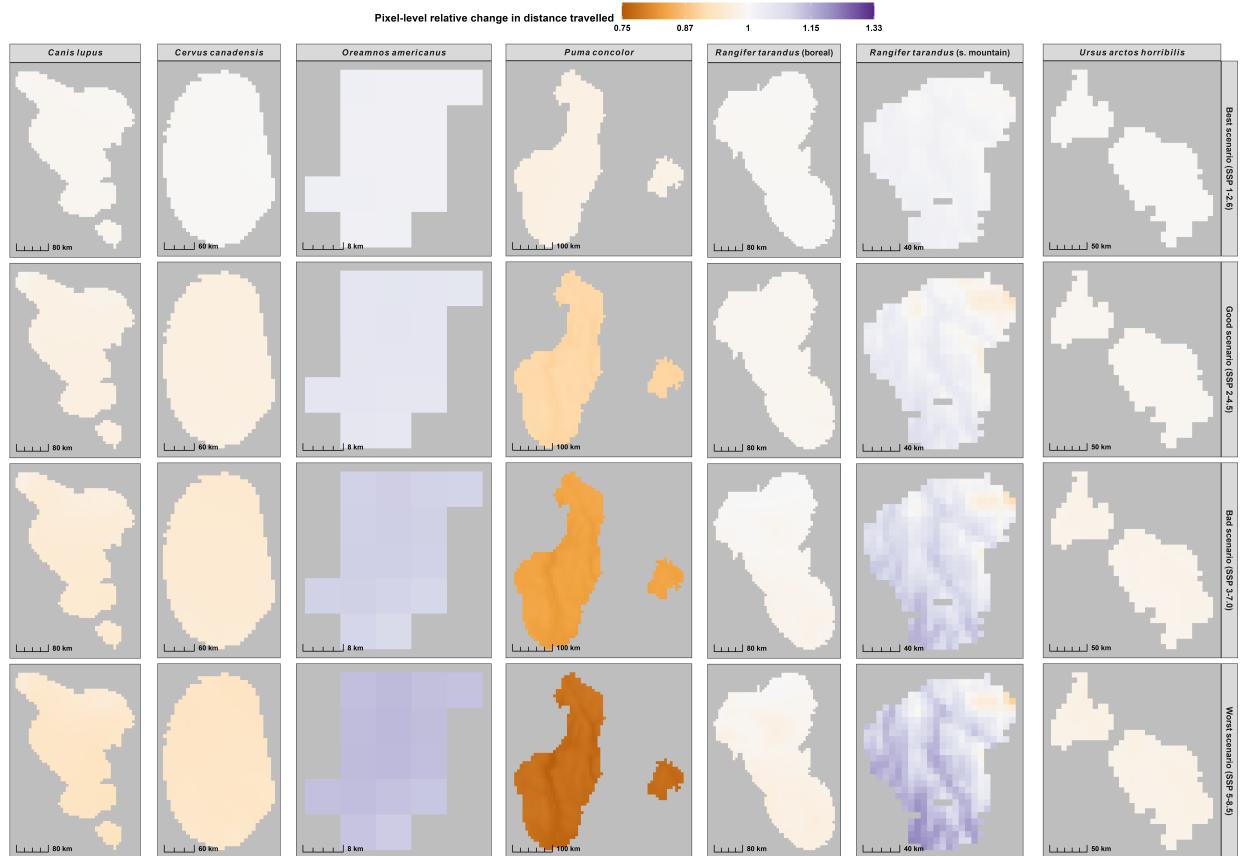


Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within each species' observed extent. Shaded areas indicate the range of predicted values between the 95<sup>th</sup> and 5<sup>th</sup> percentiles. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). If the intervals are fully above the dashed line, at least 90% of the estimated means increased, relative to the each pixel's average of the four climate SSPs in 2025. Similar conclusions can be drawn regarding a decrease if the ribbons are below the dashed line. The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.



**Figure 6: Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each pixel's average distance in 2025 across all four scenarios (i.e., not relative to other pixels). 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 0.50 to 1.56). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest density. All maps are shown with a BC Albers projection (EPSG:3005).

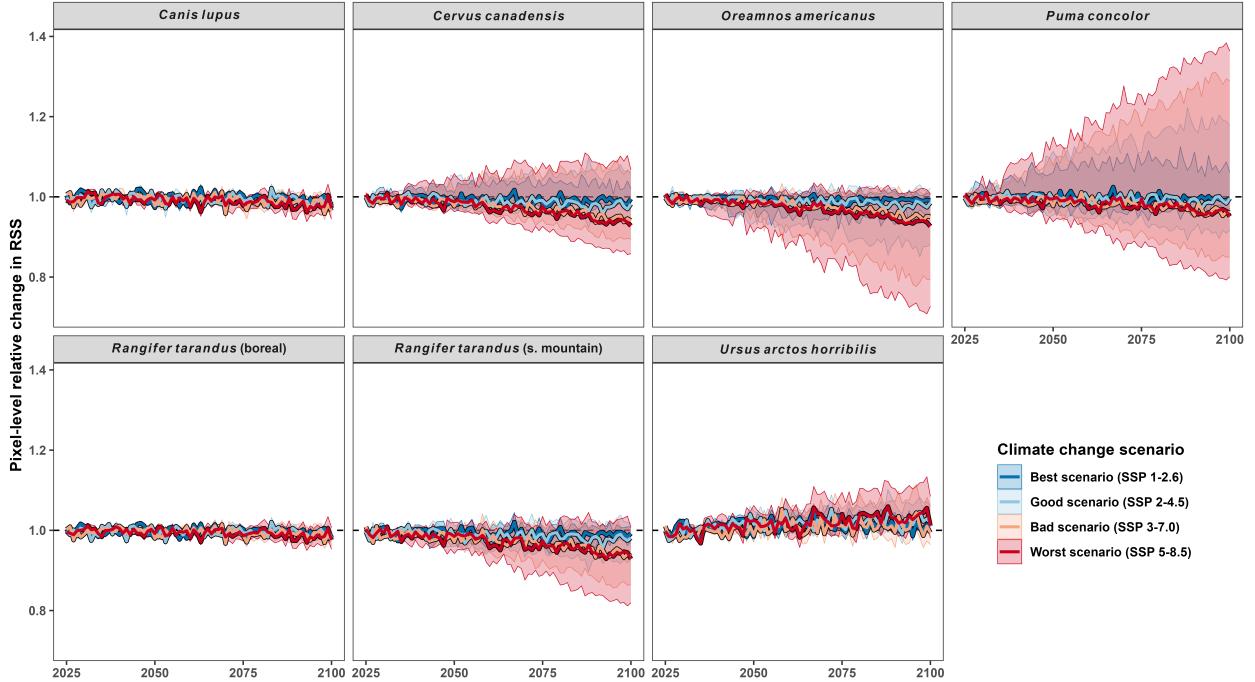
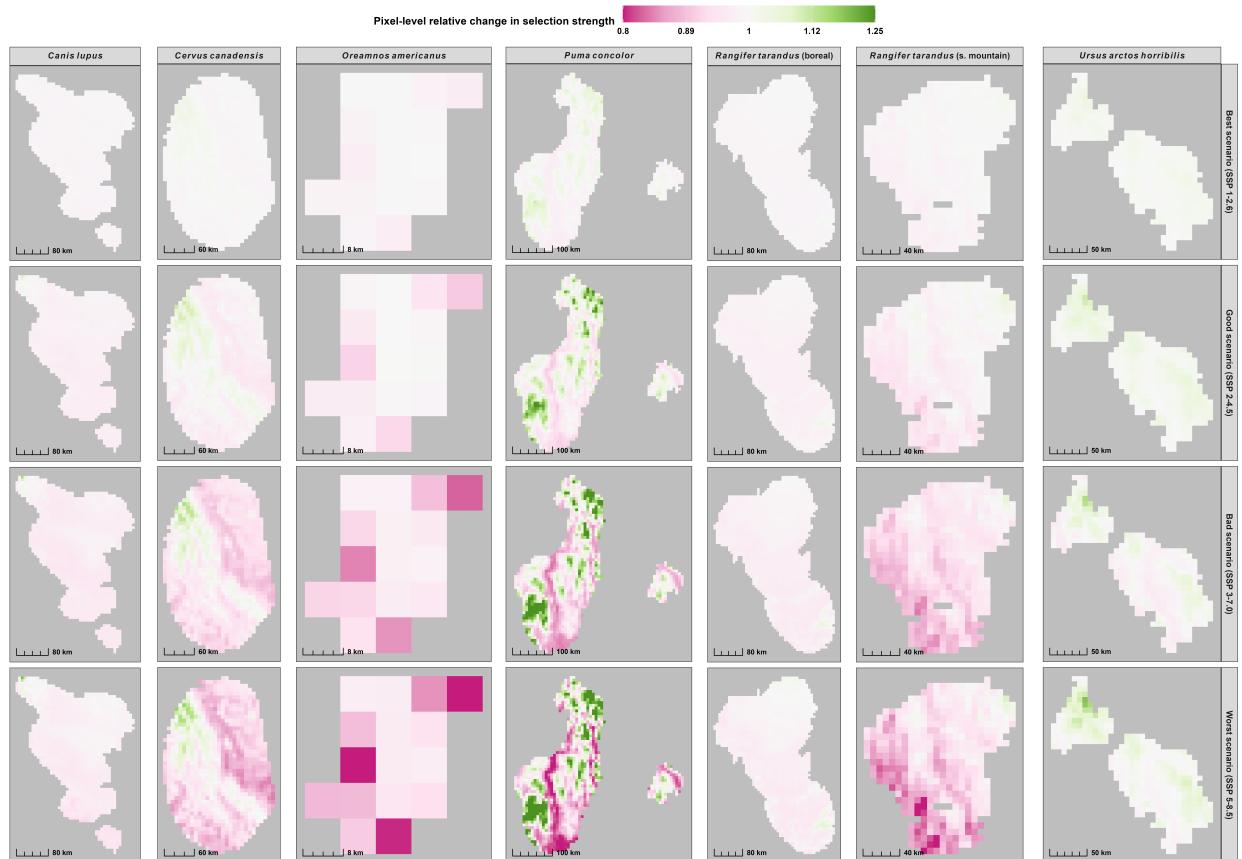


Figure 7: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within each species’ observed extent within BC, while the ribbons indicate the range between the 95<sup>th</sup> and 5<sup>th</sup> percentiles in RSS. Changes are relative to each location’s mean RSS in 2025 across the four Shared Socioeconomic Pathways (SSPs).

## 341 5 Discussion

342 We have demonstrated that temperature is an important determinant of whether, how,  
 343 and where large mammals move, even while accounting for seasonality (e.g., changes in  
 344 photoperiod, hormones, and resources). Disentangling temperature from other drivers is  
 345 important for predicting how changes in climate will affect mammalian movement when  
 346 other drivers remain approximately constant. However, predicting mammals’ responses to  
 347 climate change becomes increasingly complex as habitats warm and animals are exposed to  
 348 increasingly frequent conditions that are both extreme and novel.

349 Predicting mammals’ responses at the data-scarce fringes of the surface plots in Figs. 3  
 350 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.  
 351 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;  
 352 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,  
 353 and/or prey can often be substantially different from the behaviour at typical temperatures.



**Figure 8: 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 (i.e., not relative to other pixels). 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 0.66 to 1.86). All maps are shown with a BC Albers projection (EPSG:3005).

354 As extreme temperature events become more frequent and prolonged throughout the year  
355 (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-  
356 haviours that may alter community structures and behaviours, both during such events and  
357 afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,  
358 changes in climate and phenology impact the life history and behaviour of many hibernat-  
359 ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality  
360 (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

361 Changes in animal movement behavior may also alter the frequency and intensity of  
362 human-wildlife conflict, especially with the addition of growing pressures from human de-  
363 velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At  
364 the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,  
365 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease  
366 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being  
367 preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;  
368 Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;  
369 Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences  
370 for population and ecosystem structures and dynamics as prey, predators, and competitors  
371 experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*  
372 *al.*, 2011).

373 Our ability to respond changes in climate is contingent on our ability to prepare for and  
374 predict change. However, predicting animal behaviour becomes increasingly complicated as  
375 the conditions animals are exposed to deviate from current, typical conditions, especially  
376 when responses are nonlinear and data are sparse. Consequently, we do not present our re-  
377 sults as a definitive guide to how mammals in western Canada will respond to climate change.  
378 Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement  
379 rates and habitat selection depend on temperature and (2) how one can estimate mammals'  
380 changes in movement behaviour due to climate change. Additionally, communicating un-

<sup>381</sup> certainty in one's estimates is crucial in assessing risk probabilistically, and appropriate  
<sup>382</sup> measures of uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre &  
<sup>383</sup> Landis, 2012; Czado & Brechmann, 2014).

<sup>384</sup> *Achieving the “30 by 30” goal will require international collaboration (Huang & Zhai,  
385 2021) as well as active partnership with local Peoples, especially Indigenous Peoples (Wong  
386 et al., 2020; Lamb et al., 2023). Understanding the consequences of climate change on mam-  
387 mals’ movement behaviour is a first step towards proactively responding to how mammals will  
388 respond to human-induced rapid environmental change (Sih et al., 2011; Williams & Blois,  
389 2018). In the following sections, we discuss the implications of our results in more detail.  
390 We then expand on consequences for conservation during the 21<sup>st</sup> century and considerations  
391 for future studies.*

## <sup>392</sup> 5.1 Effects of temperature on movement rates

<sup>393</sup> The heterogeneity mammals’ responses to temperature suggests that ecological communities  
<sup>394</sup> will respond to change in complex and interconnected ways. Although our models do not  
<sup>395</sup> account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that  
<sup>396</sup> warmer temperatures cause many species to alter their daily and seasonal activity patterns  
<sup>397</sup> (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C,  
<sup>398</sup> cougars moved most at night, but when temperatures were below 0°C they tended to move  
<sup>399</sup> more throughout the day. Throughout the year, they adapted their tolerance to temperature  
<sup>400</sup> and moved less when it was relatively hot (for a given time of year), especially in spring and  
<sup>401</sup> summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and  
<sup>402</sup> boreal caribou when summer temperatures were above 20°C suggests that the increasingly  
<sup>403</sup> common and intense heat waves across western Canada will have community-wide impacts  
<sup>404</sup> on movement rates, encounter rates, and potentially community structure (Martinez-Garcia  
<sup>405</sup> et al., 2020). More work is necessary on quantifying interspecific responses to temperature,  
<sup>406</sup> including the effects of temperature on predation rates (but see: Cunningham et al., 2021;

<sup>407</sup> Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme  
<sup>408</sup> heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and  
<sup>409</sup> timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,  
<sup>410</sup> 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at  
<sup>411</sup> the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially  
<sup>412</sup> since landscape changes will likely depend not only on the direct effect of temperature but  
<sup>413</sup> also on cascading changes in the availability and unpredictability of resources (McLellan &  
<sup>414</sup> McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

<sup>415</sup> **5.2 Effects of temperature on habitat selection**

<sup>416</sup> As with the effects of temperature on movement rates, the heterogeneity of temperature  
<sup>417</sup> effects on species' habitat selection indicates that efficient and proactive habitat conservation  
<sup>418</sup> will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
<sup>419</sup> physiological responses to temperature that may impact movement, such as changes in the  
<sup>420</sup> phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or  
<sup>421</sup> behaviour (e.g., migration, food caching), other than as direct responses to temperature.  
<sup>422</sup> Consequently, the behavioural changes we present should be interpreted carefully. While  
<sup>423</sup> some seasonal cycles do not depend directly on temperature and may thus not be impacted  
<sup>424</sup> directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the  
<sup>425</sup> predictions we present also rely on the assumption that mammals will not adapt these  
<sup>426</sup> seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage  
<sup>427</sup> availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important  
<sup>428</sup> to stress the distinction between habitat selection and quality. While animals tend to select  
<sup>429</sup> for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can  
<sup>430</sup> also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,  
<sup>431</sup> 2021).

432 **5.3 Predicted changes in movement during the 21<sup>st</sup> century**

433 Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on  
434 Biological Diversity, 2022) will require careful planning but often also rapid action. In the  
435 case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the  
436 end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment  
437 and Climate Change, 2024). Additionally, efficient and effective conservation will require  
438 collaboration with Indigenous and local communities to ensure Treaties are respected in the  
439 process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,  
440 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,  
441 2021).

442 The diversity in predicted changes in movement behavior by 2100 (both across species  
443 and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the  
444 need for careful planning that incorporates not only reliable estimates of change but also  
445 pragmatic and communicable measures of uncertainty and variability around such estimates.  
446 For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-  
447 individual variation should be accounted for when deciding the location and size of protected  
448 areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly  
449 limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva  
450 *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on  
451 mammals’ movement require a holistic view of the direct effects of temperature on mammals’  
452 movement directly as well as its effects on other drivers of movement, such as forage and prey  
453 availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,  
454 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,  
455 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation  
456 among the responses of different species (and individuals), especially as populations undergo  
457 a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from  
458 human activity, including habitat fragmentation, habitat loss, and greater human presence

<sup>459</sup> in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal  
<sup>460</sup> *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and  
<sup>461</sup> likely decreases), some animals may disperse, relocate to a new habitat, or remain within  
<sup>462</sup> the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*,  
<sup>463</sup> 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

<sup>464</sup> **5.4 Species-specific considerations**

<sup>465</sup> **5.4.1 *Canis lupus***

<sup>466</sup> **5.4.2 *Cervus canadensis***

<sup>467</sup> **5.4.3 *Oreamnos americanus***

<sup>468</sup> **5.4.4 *Puma concolor***

<sup>469</sup> attraction for disconnected patches of high elevation could lead to fragmentation or traps

<sup>470</sup> **5.4.5 *Rangifer tarandus* (boreal)**

<sup>471</sup> Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000  
<sup>472</sup> m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and  
<sup>473</sup> (2) crossing the 500 m to > 1,000 m regions is safe and attractive

<sup>474</sup> **5.4.6 *Rangifer tarandus* (s. mountain)**

<sup>475</sup> HRSFs do not account for migratory behavior due to reproduction or predation risk

<sup>476</sup> **5.4.7 *Ursus arctos horribilis***

<sup>477</sup> **5.5 Considerations for future studies**

<sup>478</sup> Our work highlights three central considerations for future research: (1) telemetry sam-  
<sup>479</sup> pling rates should be designed primarily in relation to the movement timescales of the species

480 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of indi-  
481 viduals tracked and the length of each telemetry should depend not just on population size  
482 but also the rate of environmental change, and (3) predicting changes in movement behaviour  
483 becomes highly complex when responses are nonlinear, especially when changes depend on  
484 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses  
485 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

486 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,  
487 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-  
488 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.  
489 This dependency is because coarsely-sampled movement data contains information on large-  
490 scale movements (range crossings, migrations) but not fine-scale movements, including first-  
491 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour  
492 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-  
493 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement  
494 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional  
495 examples of how the frequency of location data affects the results that can be inferred by  
496 modeling movemet behavior. Consequently, we suggest being cautious when comparing esti-  
497 mated movement behaviours across species, even though all predictions have been corrected  
498 to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Ide-  
499 ally, sampling schedules should be fine enough to reconstruct animals' movement movement  
500 paths. Good estimates of an animal's speed and trajectory require telemetry locations to  
501 be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so  
502 that, on average, the dataset contains multiple locations in between changes in direction.  
503 What constitutes a change in direction depends on what movement scale one is investigating.  
504 Small-scale movements and first-order spatial selection will require more frequent sampling  
505 than migratory movement or second-order and third-order spatial selection. While `ctmm`  
506 movement models are scale-invariant in that any model can be scaled to larger or smaller

507 areas and timescales, the model estimates are not independent of the scale of the sampling  
508 frequency.

509 When landscapes are relatively predictable across years, a larger number of sampled  
510 individuals is likely preferable over the duration of each tracking period. The greater number  
511 of tracked animals allows one to quantify the variance across individuals, including the  
512 range of conditions and environments that individual animals are in. A good estimate of  
513 inter-individual variance provides better coefficient estimates along with more appropriate  
514 measures of uncertainty. However, when conditions across years are stochastic, multi-year  
515 telemetries allow one to better estimate inter-annual variation without conflating it with  
516 inter-individual differences. Given the widespread, rapid, and accelerating changes across  
517 many habitats (particularly at high elevations and at high latitudes), we suggest researchers  
518 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while  
519 increasing the ranges of temperatures each individual is observed in. Longer observational  
520 periods can also improve the chances of observing different community dynamics, such as  
521 shifts in predator-prey dynamics.

522 Temperature affects many aspects of mammalian physiology and behavior, including en-  
523 ergetics, sleep, and movement behavior. Climatic changes during the last two centuries have  
524 exposed many mammals to novel and increasingly extreme environmental conditions that  
525 have led to visible changes that impact not only individuals but also ecological and human  
526 communities. However, quantifying the effects of climate change is often complex, espe-  
527 cially as conditions become increasingly different and extreme events become increasingly  
528 common. Accurately quantifying the nonlinear effects of temperature on when, how, and  
529 where mammals move requires careful data collection and model design. We have presented  
530 a multi-species analysis of the effects of temperature on mammalian movement rates and  
531 habitat selection in hopes that other researchers can leverage this framework and models  
532 to expand our understanding of how temperature affects the movement behavior of other  
533 species, including smaller mammals, more elusive species, and non-mammal animals. Un-

derstanding of how temperature affects each species in a community will allow us to begin making community-level inferences of how temperature will affect intra-specific interactions from a movement behavior perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*, 2020). While adopting such a perspective is surely not simple, it would result in more complete estimates of the effects of climate change on community ecology, particularly when species are exposed to rapid change in many important variables. Future work should explore the effects of temperature on movement behavior while accounting for finer-scale and species specific variables that were not accounted for in this study. Examples of these include temporally dynamic measures of forest type and age, canopy density, competitive pressures, forage availability, and predator avoidance, or environmental stochasticity. However, many of these data not available, so we also suggest that more work be done on quantifying such measures using spatiotemporally dynamic models and sufficiently fine resolutions.

## 6 Author contributions

SM performed the data cleaning, ran the analyses, and wrote the majority of the manuscript. CHF wrote code for estimating instantaneous movement speeds. MJN conceived of the project idea and supervised SM throughout the project. All other authors contributed telemetry data and contributed to the interpretation of the results for their species of interest. All authors contributed to reviewing the manuscript.

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