

The heat is on: Rising temperatures alter how and where mammals  
move

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## Abstract

Widespread warming during the last century has caused many terrestrial mammals to change how and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have estimated the effects of temperature on mammalian movement behaviour, but many did not disentangle them from seasonal behaviour cycles. Consequently, it is still unclear how mammals will adapt their movement behaviour 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 movement rates and habitat selection of six large-bodied mammalian species throughout western Canada between 1998 and 2023. We show that temperature is a strong determinant of how and where mammals move, and we predict that climate change will have significant impacts on mammals' movement rates and habitat selection throughout the 21<sup>st</sup> century. We found that species did not respond uniformly to rising temperatures, so community-level responses will likely be complex as some species move more and others less. Median habitat selection strength decreased for all species, but some species showed increased selection strength for higher altitudes. Consequently, our results suggest that all six species may shift their range in the coming decades as their selection strength for their current ranges weakens. As climate change exposes mammals to novel environmental conditions, predicting changes in mammalian behaviour and community structure will become crucial for effectively and proactively understanding mammalian movement behaviour and protecting high-quality habitat. We thus present our work using a flexible approach that can be adapted for different species and spatiotemporal scales, and we conclude by providing suggestions for future research, with particular attention to the study design, statistical modeling, and forecasting.

## <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 optimize resource use (e.g., food, water, shelter; Charnov,  
<sup>4</sup> 1976; Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use  
<sup>5</sup> (Schwerdt *et al.*, 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-  
<sup>6</sup> Herrera *et al.*, 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024).  
<sup>7</sup> However, ambient temperature affects mammals' movement rates by altering the energetic  
<sup>8</sup> cost of movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016;  
<sup>9</sup> Jahn & Seebacher, 2022) and extreme temperatures can reduce movement rates and cause  
<sup>10</sup> physiological damage (Heten *et al.*, 2014; Dyer *et al.*, 2023). Animals may search for a short-  
<sup>11</sup> term buffer from extreme heat or cold via thermal refugia (Hannah *et al.*, 2014; Elmore *et*  
<sup>12</sup> *al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), which  
<sup>13</sup> may even be preferred over forage abundance (Hall *et al.*, 2016). By altering mammals'  
<sup>14</sup> movement speed and habitat use (jointly, their movement behaviour: Nathan *et al.*, 2008,  
<sup>15</sup> 2022), ambient temperature also affects the consequences of movement behaviour (Alston  
<sup>16</sup> *et al.*, 2020; Giroux *et al.*, 2023), such as encounter rates with resources (Mezzini *et al.*,  
<sup>17</sup> 2025), humans (Weststrate *et al.*, 2024), predators, prey, or competitors (Martinez-Garcia  
<sup>18</sup> *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). Behavioural changes to temperature  
<sup>19</sup> are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018) and extreme heat  
<sup>20</sup> (Powers *et al.*, 2017; Alston *et al.*, 2020; Giroux *et al.*, 2023; Verzuh *et al.*, 2023).

<sup>21</sup> Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood &  
<sup>22</sup> Huber, 2010). While extreme cold often leads to reduced movement, provided that individ-  
<sup>23</sup> uals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou *et al.*,  
<sup>24</sup> 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological damage  
<sup>25</sup> in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021;  
<sup>26</sup> Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly when

27 ambient temperatures are near or above their body temperature, they are particularly sen-  
28 sitive to extreme heat, especially with increasing body size (Dyer *et al.*, 2023; Verzuh *et al.*,  
29 2023). Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature  
30 specialists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tri-*  
31 *dactyla*: Giroux *et al.*, 2023), while species that experience wide ranges of temperature vari-  
32 ation (i.e., ‘temperature generalists’) can adapt more easily to change (Levins, 1974; Botero  
33 *et al.*, 2015; Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they  
34 are subject to changes that are more severe (McCain, 2019; Rantanen *et al.*, 2022), affect  
35 many factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource  
36 availability: Polazzo *et al.*, 2024), or are too rapid and severe to respond within a lifetime  
37 or a few generations (Levins, 1974; Gienapp *et al.*, 2008; Fuller *et al.*, 2016; Xu *et al.*, 2021).

38 In the last century, many ecosystems experienced widespread warming that resulted in  
39 milder and shorter winters, hotter and longer summers, and a greater risk of extremely high  
40 temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will  
41 continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et*  
42 *al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense  
43 extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and frag-  
44 mentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear  
45 how or whether species will be able to respond to climate change in the current century  
46 (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations  
47 fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically  
48 incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and  
49 responding to future changes require a comprehensive understanding of how temperature  
50 will affect how and where mammals move, as well as the implications such changes will have  
51 on species’ adaptability and overall community structure (Cunningham *et al.*, 2021). Re-  
52 cent work has documented the effects of climate change on mammals’ ranges (Leclerc *et al.*,  
53 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and movement behaviour (McCain, 2019;

54 Cunningham *et al.*, 2021; Melin *et al.*, 2023). However, there remains a need for fine-scale  
55 estimates of the effects of temperature on mammals' movement behaviour and quantitative  
56 predictions of changes in movement behaviour with climate change in the current century  
57 (IPCC, 2023).

58 Western Canada is currently experiencing rapid widespread warming (Turner & Clifton,  
59 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu *et al.*,  
60 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et al.*, 2023). As  
61 we approach the deadline for the Kunming-Montreal Global Biodiversity Framework (i.e.,  
62 the "30 by 30" initiative), a global effort to conserve 30% of the world's lands and oceans by  
63 2030 (Convention on Biological Diversity, 2022), Canadian decision makers must understand  
64 which areas will be of greatest value for maximizing and protecting biodiversity not only for  
65 current conditions but future decades, too. Failing to understand how climate change will  
66 affect mammalian movement behaviour will hinder our ability to respond to the current  
67 climate crisis and make decisions that are viable in the long term. Furthermore, under-  
68 standing how temperature affects individual species is the first step towards understanding  
69 how temperature impacts the community dynamics (Hegel *et al.*, 2010; Cunningham *et al.*,  
70 2021; Carbeck *et al.*, 2022) and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012;  
71 Merkle *et al.*, 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and how these changes will  
72 impact mammals in the coming decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et*  
73 *al.*, 2024).

74 In this paper, we quantify the effects of proximal air temperature on mammalian move-  
75 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial  
76 mammal species in western Canada (wolves: *Canis lupus*, elk: *Cervus canadensis*, moun-  
77 tain goats: *Oreamnos americanus*, cougars: *Puma concolor*, boreal and southern mountain  
78 caribou: *Rangifer tarandus*, and grizzly bears: *Ursus arctos horribilis*; Table 1). Using over  
79 25 years of telemetry data throughout a large spatial range of western Canada and hourly  
80 air temperature data, we estimate how these mammals altered their probability of mov-

81 ing, speed when moving, and habitat selection in response to temperature. We then pair  
 82 the estimated responses with climate change projections to forecast the species' movement  
 83 behaviour during the 21<sup>st</sup> century under different climate-change scenarios (referred to as  
 84 Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss the consequences of  
 85 these changes in movement behaviour at the individual, population, and community levels.  
 86 We also provide directions for future research and solutions for overcoming some common  
 87 data limitations.

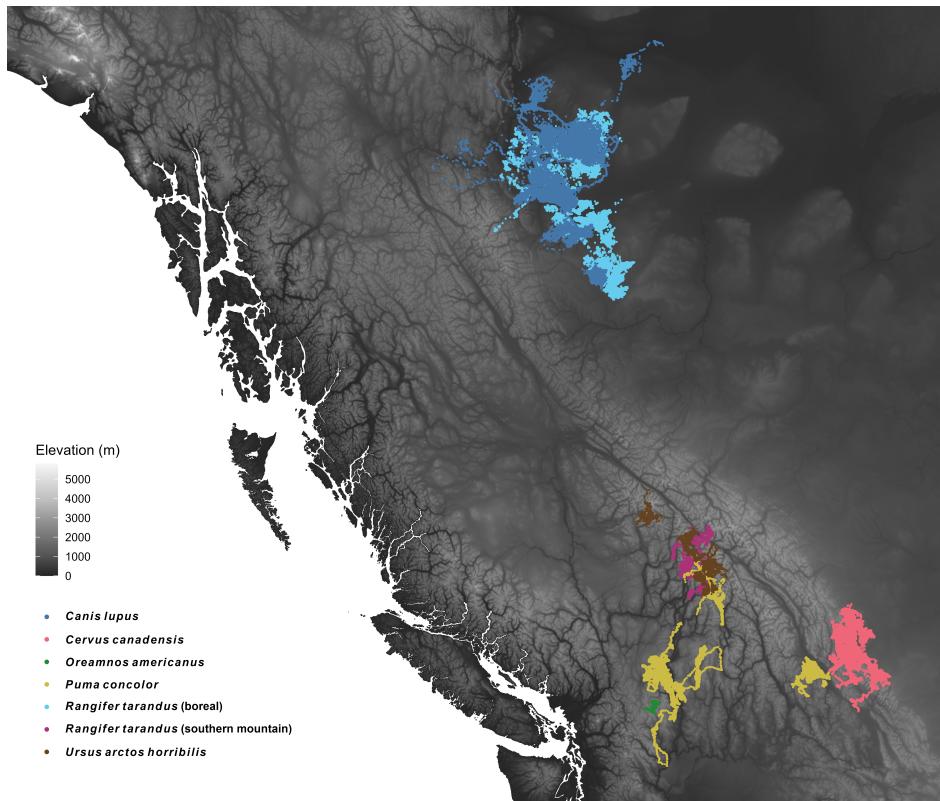


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Summary statistics of each species' set of GPS data, including: the start and end of each set of GPS telemtries, the median sampling interval ( $\Delta t$ ; stratified by animal), number of animals (Animals), and number of animals with finite speed estimates (Has speed).

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

Species	Start	End	$\Delta t$ (hours)	Animals	Has speed
<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

## 88 2 Methods

### 89 2.1 Datasets used

90 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry  
 91 data (Fig. 1); (2) historical hourly air temperature from the ERA5 reanalyzed dataset (Euro-  
 92 pean Center for Medium-range Weather Forecasting; Hersbach *et al.*, 2023); (3) temporally  
 93 static rasters of percent forest cover, elevation, and distance from water; and (4) climate  
 94 change projections under four Shared Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017).  
 95 While we acknowledge there are other important variables (e.g., forest type, structure, and  
 96 age; terrain slope and aspect), we limited our models to only use three simple variables  
 97 for the sake of parsimony and comparability across species. See the discussion section for  
 98 additional detail on the advantages and limitations of using such simple models.

#### 99 2.1.1 GPS telemetry data

100 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
 101 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022). Boreal caribou (*Rangifer*  
 102 *tarandus*) and wolf (*Canis lupus*) telemtries were acquired from a data repository of the  
 103 British Columbia Oil and Gas Research and Innovation Society (BC OGRIS) that was col-  
 104 lected as part of the boreal caribou radio-collaring program of the BC OGRIS Research  
 105 and Effectiveness Monitoring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON**  
 106 **OTHER TELEMETRY DATA.** From the full set of telemetry data, we removed a total

107 of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspect-  
108 ing diagnostic plots of (1) distance from the median location, (2) straight-line displacement  
109 between locations, (3) turning angle, and (4) time interval between consecutive points. Par-  
110 ticular attention was paid to points with large turning angles ( $\gtrapprox 170^\circ$ ) and excessively high  
111 straight-line displacement, especially if antecedent and subsequent points indicated relatively  
112 stationary behaviour (Appendix A).

### 113 2.1.2 Historical temperature data and climate change projections

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

120 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA (v.  
121 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly tempera-  
122 tures from 2020 to 2100 at a  $0.08^\circ$  spatial resolution. Since the climate projections only pro-  
123 vided monthly means and ranges but no measures of variance or distributional assumptions,  
124 we used the historical data for western Canada from 1998 to 2023 (extremes included) to esti-  
125 mate the monthly variation in temperature, which we defined as  $\sigma_T^2$ , the variance at location  
126  $\langle x, y \rangle$  in month  $m$  for each year (e.g., the variance at coordinates  $\langle -119.40, 49.94 \rangle$  in April  
127 2005). We then modeled the estimated variance using a Generalized Additive Model (GAM)  
128 for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;  
129 section 7.9 in Wood, 2017) using the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear  
130 predictor for the location (i.e., the mean) included smooth terms of: each year's estimated  
131 within-pixel monthly mean temperature ( $\hat{\mu}_T$ ), month ( $m$ ), a two-dimensional smooth of spa-  
132 tial coordinates  $\langle x, y \rangle$ , and a tensor product interaction term of month and space to allow

133 for seasonal terms to vary smoothly over space. The linear predictor for the scale term,  
 134 which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included  
 135 smooth terms of the monthly mean temperature, month, and space. We did not include  
 136 smooth terms of year to avoid unrealistic projections when extrapolating beyond past 2023.  
 137 The model was thus

$$\left\{ \begin{array}{l} \sigma_T^2 \sim \text{Gamma}(\mu_{\sigma_T^2}, \nu_{\sigma_T^2}) \\ \mathbb{E}(\sigma_T^2) = \mu_{\sigma_T^2} \\ \mathbb{V}(\sigma_T^2) = (\mu_{\sigma_T^2})^2 / \nu_{\sigma_T^2} \\ \log(\mu_{\sigma^2}) = \beta_{L,0} + f_{L,1}(\mu_T) + f_{L,2}(m) + f_{L,3}(x, y) + f_{L,4}(x, y, m) \\ \log(\nu_{\sigma^2}) = \beta_{S,0} + f_{S,1}(\mu_T) + f_{S,2}(m) + f_{S,3}(x, y) \end{array} \right. , \quad (1)$$

138 where  $\mu_{\sigma_T^2}$  and  $\nu_{\sigma_T^2}$  indicate the location and scale parameters of the gamma distribution of  
 139  $\sigma_T^2$ , and together they determine the variance of  $\sigma_T^2$ , indicated as  $\mathbb{V}(\sigma_T^2)$ . Functions  $f_{L,j}$  and  
 140  $f_{S,j}$  indicate the  $j^{\text{th}}$  smooth functions for the location and scale parameters, respectively.  
 141 To ensure the smooth functions of month,  $f_{L,2}(m)$  and  $f_{S,2}(m)$ , joined smoothly between  
 142 December and January, the terms use cyclic cubic spline bases. The spatial terms used two-  
 143 dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood  
 144 (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood  
 145 (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information  
 146 on the code used to fit the model.

147 We simulated hourly variation in future years by assuming hourly temperature followed  
 148 a normal distribution with mean specified by the monthly **climatenetR** climate projections  
 149 and variance as specified by the gamma GMLS. For each month within each year from  
 150 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the  
 151 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the  
 152 (normalized) Gaussian probability density for each quantile.

153 **2.1.3 Resource rasters**

154 We estimated percent forest cover and distance from water using the rasters created by  
155 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
156 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
157 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
158 raster of percent cover of open water (class 12) to a binary raster of pixels with water  
159 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance  
160 from the nearest pixel with water using the `distance()` function from the `terra` package.  
161 Finally, we obtained two digital elevation models using the `get_elev_raster()` function  
162 from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom  
163 of 6 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of  
164 0.08°) for downloading climate change projections via `climatenar`. All final rasters and  
165 code are available in the GitHub repository associated with this manuscript (see the Data  
166 Availability Statement).

167 **2.2 Estimating mammals' instantaneous speeds**

168 We modeled each animal's movement using continuous-time movement models (Fleming  
169 *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for `R`. We then  
170 estimated each mammal's instantaneous speed at each observed location by applying the  
171 `ctmm::speeds()` function on all models with finite speed estimates (415 of 433, Fleming *et*  
172 *al.*, 2014; Noonan *et al.*, 2019a). The 18 animals with insufficiently fine sampling to support  
173 movement models with finite speed were for one mountain goat, 15 boreal caribou, and two  
174 southern mountain caribou (Table 1).

175 Since `ctmm`'s movement models assume a single moving state with stochastic but non-  
176 zero speed, we corrected data-informed speeds so that the minimum instantaneous speed  
177 could be 0. We performed this correction by subtracting each model's mean speed while  
178 assuming speeds were  $\chi^2$ -distributed. The function we used is available on GitHub (see the

179 Data Availability Statement). To avoid artifacts due to excessively small, non-zero speeds,  
180 we determined whether an animal was moving or not using a  $k$ -means algorithm with 2  
181 clusters for each species' distribution of detrended speeds. When the algorithm clearly failed  
182 to discriminate between states, we estimated the split point using the inflection points in  
183 histograms of the detrended speeds (Fig. B1).

184 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

185 Ambient temperature is only one of the many drivers of mammalian movement behaviour  
186 (Fig. 2). Many species adapt their movement rates (e.g., movement frequency and speed)  
187 daily or seasonally in response to factors such as solar time, photoperiod, forage availability,  
188 reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates  
189 throughout the day and across seasons. Therefore, estimating the effects of temperature  
190 on movement rates requires accounting for how mammals' response to temperature changes  
191 with time of day and day of year (Fig. 2A; Péron *et al.*, 2017; Buderman *et al.*, 2018; Leclerc  
192 *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals' selection strength for resources depends  
193 on ambient temperature, since higher temperatures can promote a selection for refuge from  
194 heat (e.g., thicker forest cover, higher elevation, proximity to water; Attias *et al.*, 2018;  
195 Giroux *et al.*, 2023).

196 The two following sections detail the statistical framework and models we used to estimate  
197 the effect on temperature on the six species' movement behavior. To assess the importance of  
198 including temperature as an explicit covariate (as opposed to including its effects with time  
199 of day and day of year), we fit models with and without smooth effects of temperature and  
200 compared the fits of the two sets of models via analyses of deviance (a form of generalized  
201 likelihood ratio tests) following the methods of Section 3.3 in Wood (2017). See Appendix  
202 B for additional information.

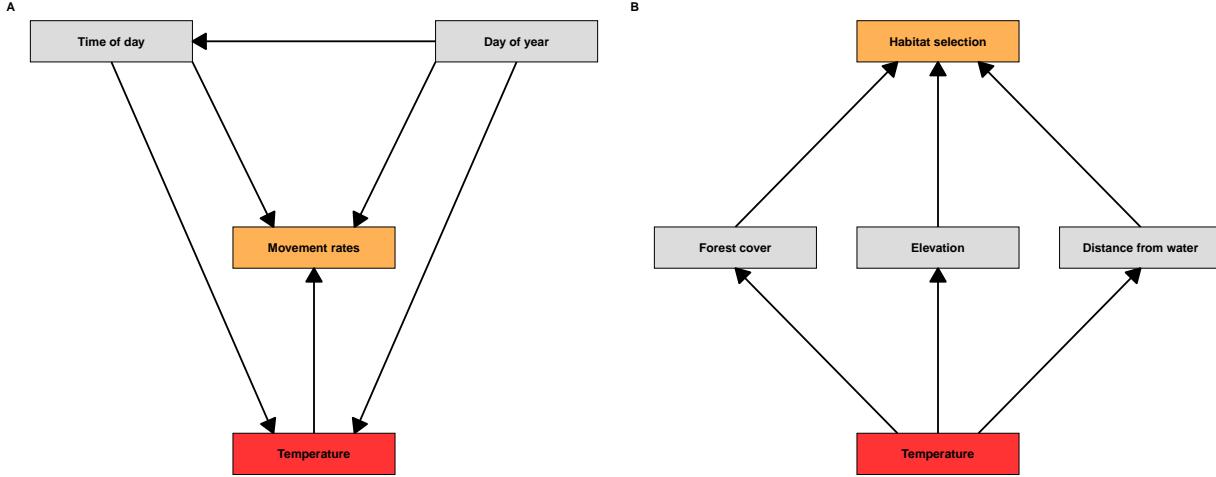


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time of day and day of year. Additionally, the effects of temperature on movement rates depend on time of day and season, since animals may respond to temperatures differently at different times of day and or days of year. Finally, the effect of time of day changes seasonally due to changes in photoperiod. (B) Similarly, habitat selection depends on the availability and selection of resources (forest cover, elevation, and distance from water), but the selection strength for each resource is conditional on temperature. For example, an animal may avoid forested areas unless it is seeking refuge from extreme temperatures.

### 2.3.1 Effects of temperature on movement rates

We estimated the effects of temperature on mammals' instantaneous movement state (moving or not) and speed when moving using two Hierarchical Generalized Additive Models (HGAMs, see Pedersen *et al.*, 2019 and Appendix B) with the `mgcv` package for R. The first HGAM estimated the probability that an animal was moving,  $P(M)$ , with a binomial family of distributions and logit link function. The second HGAM estimated an animal's speed when moving with a gamma family of distributions and log link function. We fit the models with fast Restricted Maximum Likelihood ('fREML') and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no appreciable losses to model performance (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma HGAM inform us on an animal's long-term average speed, since it is the product of the probability of moving and its average speed when moving.

The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species ( $\beta_s$ ), random intercepts for each animal ( $Z_a$ ), and species-level by smooths that allowed independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*

218 *al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific Daylight Time;  
 219 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time  
 220 of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017).  
 221 The models also had three tensor product interaction terms `by` each species: (1) day of year  
 222 and time of day, (2) temperature and time of day, and (3) temperature and day of year. These  
 223 three terms accounted for smooth changes in: (1) daily behavior across day of year, (2) the  
 224 response to temperature over time of day (e.g., changes in nocturnality), and (3) the response  
 225 to temperature over day of year (e.g., changes in coats and migration timing). Finally, two  
 226 smooth terms of log-transformed sampling interval (`dt`; hours) corrected for biases in speed  
 227 estimates arising from irregular GPS sampling intervals, since longer intervals result in lower  
 228 speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025). A global smooth term of  $\log(dt)$   
 229 accounted for the overall effect of sampling interval, while a factor-smooth interaction term  
 230 (`bs = 'fs'`) of  $\log(dt)$  and species accounted for species-level deviations from the global  
 231 term while assuming a common smoothness parameter across species (model GS in Figure 4  
 232 of Pedersen *et al.*, 2019). Formally, the model for movement state  $M$ , with  $M = 0$  indicating  
 233 no movement and  $M = 1$  indicating movement, was

$$\left\{ \begin{array}{l} M \sim \text{Bin}(p) \\ \mathbb{E}(M) = p \\ \mathbb{V}(M) = p(1-p) \\ \text{logit}(p) = \beta_s + Z_a + f_{1,s}(\text{tod\_pdt}) + f_{2,s}(\text{doy}) + f_{3,s}(\text{temp\_c}) + \\ f_{4,s}(\text{doy}, \text{tod\_pdt}) + f_{5,s}(\text{temp\_c}, \text{tod\_pdt}) + f_{6,s}(\text{temp\_c}, \text{doy}) + \\ f_7(\log(dt)) + f_{8,s}(\log(dt)) \end{array} \right. , \quad (2)$$

234 while the model for movement speed when moving (i.e.,  $M = 1$ , indicated with  $S$ ) was

$$\left\{ \begin{array}{l} S \sim \text{Gamma}(\mu_S, \nu_S) \\ \mathbb{E}(S) = \mu_S \\ \mathbb{V}(S) = \mu_S^2 / \nu_S \\ \log(\mu_S) = \beta_s + Z_a + f_{1,s}(\text{tod\_pdt}) + f_{2,s}(\text{doy}) + f_{3,s}(\text{temp\_c}) + \\ f_{4,s}(\text{doy}, \text{tod\_pdt}) + f_{5,s}(\text{temp\_c}, \text{tod\_pdt}) + f_{6,s}(\text{temp\_c}, \text{doy}) + \\ f_7(\log(\text{dt})) + f_{8,s}(\log(\text{dt})) \end{array} \right. . \quad (3)$$

235 In both models,  $\beta_s$  indicates a fixed intercept for species  $s$ ,  $Z_a$  indicates a Gaussian random  
 236 effect for animal  $a$  (of species  $s$ ),  $f_{j,s}$  indicates the  $j^{\text{th}}$  smooth function for species  $s$ , and  
 237 functions with two variables indicate tensor product interaction terms. The model code used  
 238 to fit the models is available in Appendix B.

239 **2.3.2 Effects of temperature on habitat selection**

240 We estimated the effects of temperature on each species' selection for percent forest cover  
 241 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 242 ting a Hierarchical Resource Selection Function (HRSF) for each species. We fit each HRSF  
 243 using an HGAM with a Poisson family of distributions and log link function (Appendix B;  
 244 Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the  
 245 spatiotemporal autocorrelation in the telemetry locations by weighting each point based on  
 246 the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noo-  
 247 nan *et al.*, 2019b; Alston *et al.*, 2022) to produce estimates of second-order habitat selection  
 248 (Johnson, 1980). Quadrature points were determined using the raster cells in each animal's  
 249 99.9% AKDE percentile and given a weight of 1. The number of quadrature locations greatly  
 250 outnumbered the number of observed locations (Fig. B12), especially after accounting for  
 251 the AKDE weights (Fig. B13).

252 Each species' model had the same structure:

$$\left\{ \begin{array}{l} C \sim \text{Pois}(\lambda) \\ \mathbb{E}(C) = \mathbb{V}(C) = \lambda \\ \log(\lambda) = f_1(\text{forest_perc}) + f_2(\text{elevation_m}) + f_3(\text{dist_water_m}) + \\ Z_a + f_{4,a}(\text{forest_perc}) + f_{5,a}(\text{elevation_m}) + f_{6,a}(\text{dist_water_m}) + \\ f_7(\text{forest_perc}, \text{temp_c}) + f_8(\text{elevation_m}, \text{temp_c}) + \\ f_9(\text{dist_water_m}, \text{temp_c}) + f_{10}(\text{temp_c}) + f_{11,a}(\text{temp_c})) \end{array} \right. , \quad (4)$$

253 where  $O$  indicates whether an animal was observed ( $O = 1$ ) or not ( $O = 0$ ), and the species-  
254 level indices are omitted for readability, but each term in the model can be assumed to be  
255 species-specific. Smooth effects of percent forest cover (`forest_perc`), elevation (`elev_m`),  
256 and distance to water (`dist_water_m`) accounted for the species-level selection strength  
257 for each resource. A Gaussian random effect for each individual animal ( $Z_a$ ) corrected for  
258 uneven sampling across individuals, while factor-smooth interaction terms for each animal  
259 ( $f_{j,a}$ ) accounted for animal-level resource selection (i.e., individual-level deviations from the  
260 species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction terms of the three  
261 resources and temperature (`temp_c`) estimated the smooth change in resource selection at  
262 different temperatures. Finally, marginal smooth terms of temperature and factor-smooth  
263 interaction terms of temperature and animal accounted for species- and individual-level  
264 sampling biases at different temperatures (e.g., sampling more during warm periods).

### 265 3 Results

266 Overall, 2.6% of GPS locations had temperatures lower than  $-20^{\circ}\text{C}$ , while 6.5% had tem-  
267 peratures above  $20^{\circ}\text{C}$ , and temperature ranges differed across species (Table 2, Fig. B2).  
268 Sampling interval affected estimates of probability as well of as speed when moving (Fig.

269 B8). Consequently, we present all results while predicting specifically for one-hour sam-  
 270 pling intervals. At 0°C, species differed in mean probabilities of moving ( $\hat{P}(M)$ ; range:  
 271 0.05 – 0.31), mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1)$ ; range: 0.42 – 2.67 km/h), and mean  
 272 distance traveled (i.e.,  $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$ , range: 0.04 – 0.61 km/h; Table 2). Griz-  
 273 zly bears had the lowest movement frequency ( $\hat{P}(M) \approx 0.05$ ), while wolves and cougars  
 274 moved most often ( $\hat{P}(M) \geq 0.22$ ). Mountain goats and southern mountain caribou moved  
 275 the slowest ( $\hat{\mathbb{E}}(S|M = 1) \approx 0.43$  km/h), while wolves had the highest mean speed when  
 276 moving ( $\hat{\mathbb{E}}(S|M = 1) \approx 2.67$  km/h). Consequently, at 0°C, wolves traveled an average of  
 277  $0.22 \times 2.67$  km/h  $\approx 0.6$  km/h; 2.5 to 16.7 times further than other species.

Table 2: Summary statistics for the observed temperatures and estimated mean movement rates at °C. The second and third columns indicate the percentage of GPS locations (after data cleaning) with temperature ( $T$ ) below -20°C and above 20°C, respectively. The subsequent columns indicate the estimated mean probability of moving ( $\hat{P}(M = 1)$ ), mean speed when moving ( $\hat{\mathbb{E}}(S)$ ; km/h), and mean distance travelled ( $\hat{P}(M = 1) \times \hat{\mathbb{E}}(S) = \hat{\mathbb{E}}(D)$ ; km/h) as estimated by models without and with temperature (i.e., (...| $T$ )), for a sampling interval of 1 hour and a temperature of  $T = 0^\circ\text{C}$ .

Species	$\hat{P}(M = 1)$							
	T < -20°C	T > +20°C	1)	$\hat{P}(M = 1 T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>C. canadensis</i>	1.7 %	13.0 %	0.16	0.17	0.57	0.57	0.09	0.10
<i>Canis lupus</i>	2.4 %	4.9 %	0.23	0.22	2.64	2.67	0.61	0.60
<i>O.</i> <i>americanus</i>	0.7 %	2.8 %	0.15	0.13	0.43	0.42	0.06	0.06
<i>P. concolor</i>	0.7 %	6.9 %	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus;</i> <i>b</i>	6.8 %	7.9 %	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus;</i> <i>sm</i>	1.3 %	3.4 %	0.11	0.11	0.43	0.42	0.05	0.05
<i>U. arctos h.</i>	0.0 %	8.4 %	0.05	0.05	0.72	0.72	0.04	0.04
Total	2.6 %	6.5 %						

278 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and  
 279 strongest for elevation. At temperatures near 0°C, wolves selected for forest cover ( $\gtrapprox 50\%$ ),  
 280 elevations near 1 km, and distances from water < 5 km; elk selected for intermediate forest  
 281 cover ( $\approx 50\%$ ), elevations between 1 and 2 km, and distances from water of 10-15 km;  
 282 mountain goats selected for sparse forest cover (< 25%), elevations near 1.5 km, and distances  
 283 from water < 5 km; cougars selected for dense forest cover ( $> 75\%$ ), an elevation of  $\sim 1$  km,

and distances from water < 7.5 km; boreal caribou selected for forest cover between 50% and 75%, 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  $\lesssim$  5 km; and grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2 km, and distances from water < 3 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 p-values  $< 2.2 \times 10^{-16}$ ; all  $\Delta AIC \geq 342$ ; Table B2 and subsequent pages in Appendix B). Accounting for temperature even 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.

### 3.1 Effects of temperature on movement rates

Species' changes in movement rates to temperature varied in both direction and magnitude (Figs. 3, B4-B6), even after accounting for differences in daily and seasonal activity (e.g., sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and indicated clear shifts in activity over time of day and day of year for all species. The models had good in-sample prediction (Fig. B7) and explained reasonably high proportions of the deviance (79.3% for the gamma model and 10.7% for the binomial model, which is relatively high for a binomial model with binary responses: see ch. 11 of McElreath, 2020). All species adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 3). The clearest example of this was cougars. In late spring (June 1<sup>st</sup>), they moved from evening to early morning if temperatures were below 20°C, but if temperatures were above 20°C they moved mostly between 3:00 and 6:00 AM. Throughout the year, they tended to move more when it was colder, but what they perceived as "colder" was relative to the time of year. All species' estimated probability of moving and speed when moving decreased with sampling intervals above 1 hour, except for cougars' speed, although the estimated

310 trends were highly uncertain (Fig. B8). Uncertainties around the estimated effects were  
 311 generally higher at extreme temperatures due to lower data availability (Figs. B4A, B5A,  
 312 and B6A).

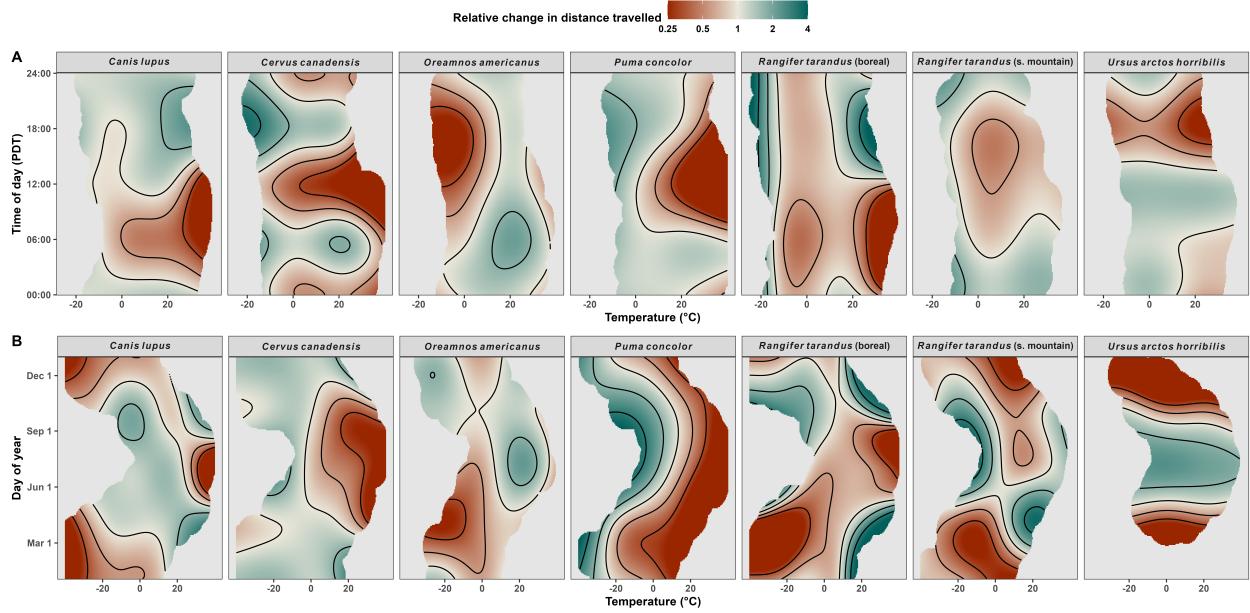
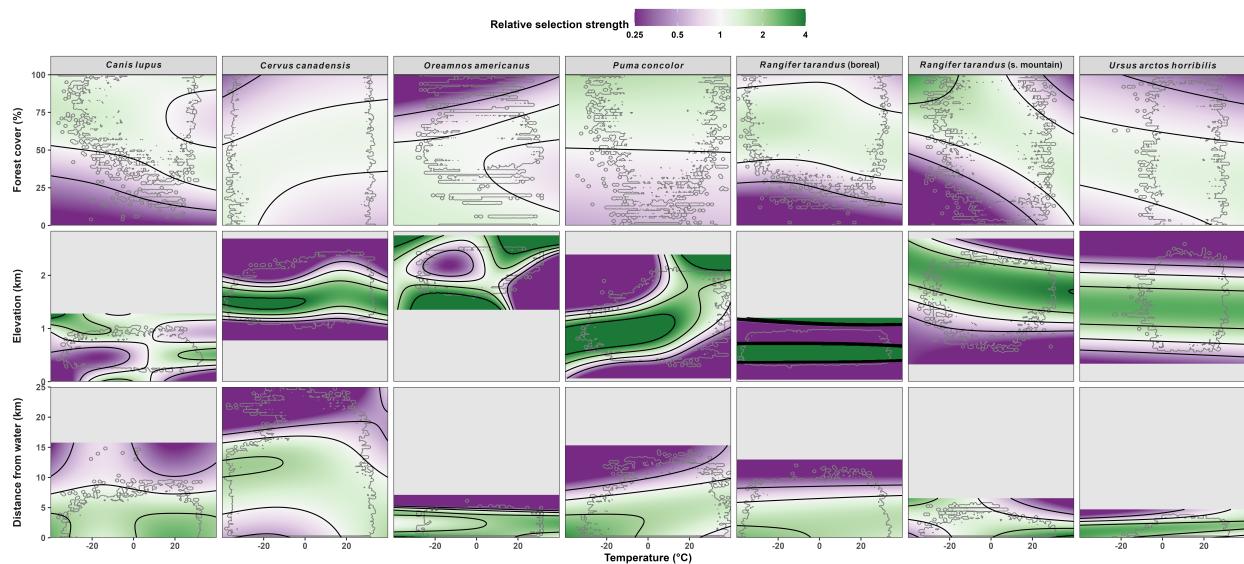


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year at 12:00 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.

### 313 3.2 Effects of temperature on habitat selection

314 Species' RSS was generally strongest for elevation and weakest for forest cover, but RSS  
 315 depended significantly on temperature for all species (all p-values  $< 2.2 \times 10^{-16}$ ; Fig. 4).  
 316 Changes in RSS with temperature were strongest for elevation and generally weakest for  
 317 distance from water, but there were no common trends across all species for any of the  
 318 three resources. All species, with the exception of cougars, exhibited clear temperature-  
 319 dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed  
 320 their preference for forested areas, while mountain goats relaxed their preference open areas  
 321 (cover < 50%). As temperatures warmed, elk and boreal caribou shifted towards more forest  
 322 cover closer to 50%, while southern mountain caribou and grizzly bears selected for areas  
 323 with 50% forest cover or less. All species shifted elevationally with temperature, although

boreal caribou ha a much sharper change in RSS across elevation. Elk, mountain goats, and cougars increased in elevation with temperature, while wolves, southern mountain caribou, and grizzly bears decreased in elevation. Wolves, elk, and southern mountain caribou moved closer to water with temperature, while mountain goats, cougars, and grizzly bears moved somewhat further away from water but remained mainly within 5-10 of water. As with movement rates, estimated RSS was generally most uncertain at extreme temperatures, for which data was scarcer (Fig. B15).



**Figure 4: Mammals' habitat selection depends on ambient temperature.** 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.

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

Predicted changes in movement rates with future climate change varied across species in both magnitude and direction, but worse SSPs always corresponded to greater absolute changes (Fig. 5). Additionally, species that were predicted to move less often did not necessarily have lower speeds when moving, and vice versa (Figs. B9 and B10). Absolute relative changes in average yearly distance travelled were small under the best-case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while the models estimated that grizzly bears would move substantially less (if at all) in late fall and winter (Figs. 3, B4),

340 the models did not explicitly account for changes in hibernation phenology. Consequently,  
 341 the climate change projections do not explicitly account for changes in energetic needs or  
 342 physiology. Projected changes in 2100 varied spatially due to spatial heterogeneity in climate  
 343 change projections (Fig. 6). Again, absolute changes were generally greatest under worse  
 344 SSPs, but the direction of change at each location also varied across SSPs (most visible in  
 345 cougars).

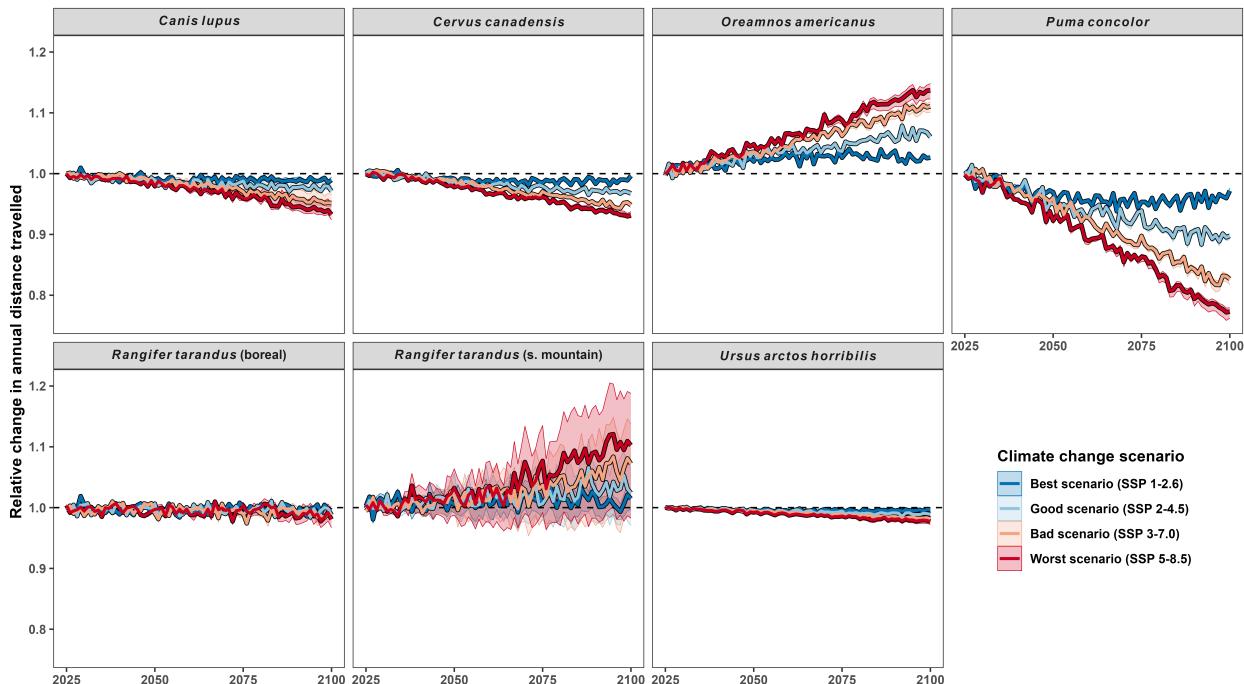


Figure 5: Species will adapt their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95<sup>th</sup> and 5<sup>th</sup> percentiles. Changes are relative to the mean predicted distance travelled at each location in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs). Values > 1 indicate an increase, while values < 1 indicate a decrease. The projections only account for changes in movement frequency and speed, and they ignore changes in physiology or movement costs.

346 Median RSS was projected to decrease over time within the each species' observed range,  
 347 but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pro-  
 348 nounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and  
 349 southern mountain caribou. Changes for boreal wolves and caribou were relatively negli-  
 350 gible. Elk, cougars, and grizzly bears were predicted to increase their selection strength  
 351 for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were  
 352 predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the

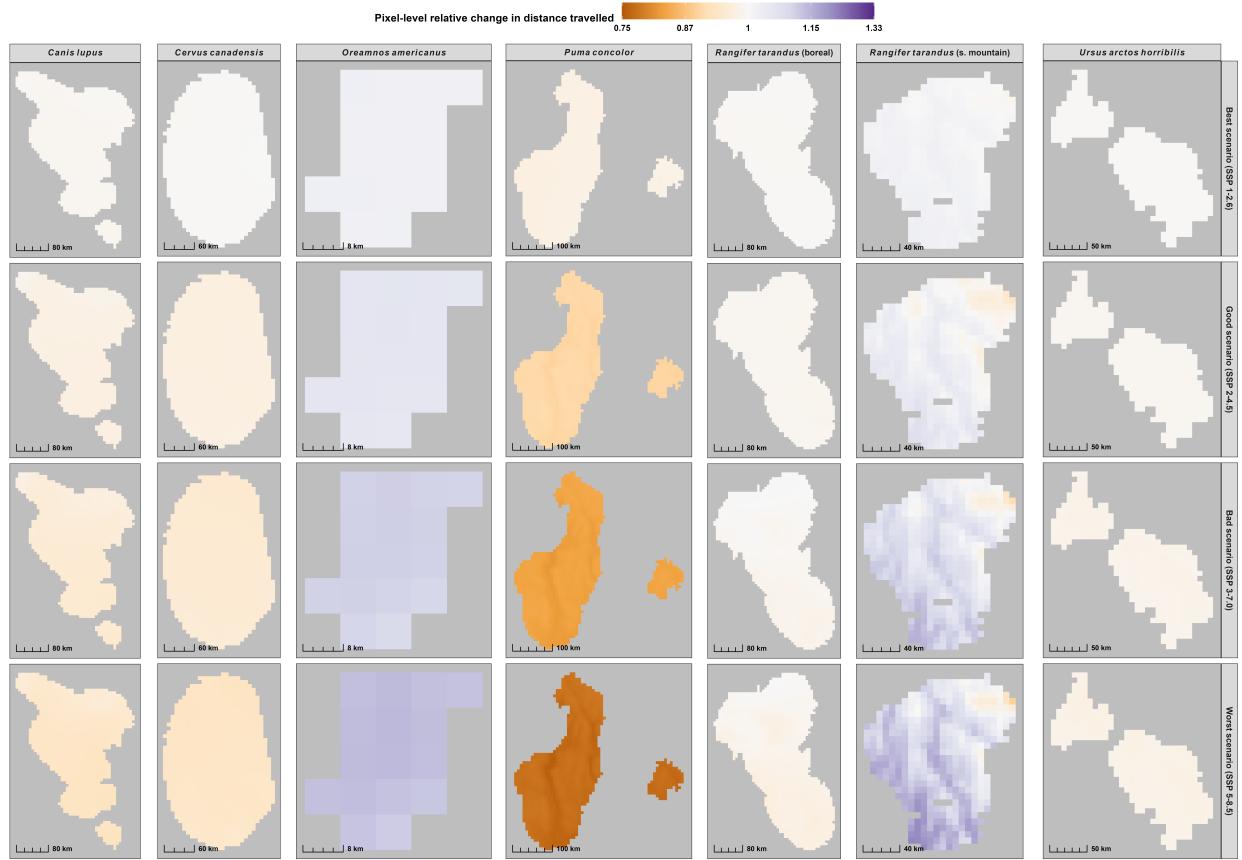


Figure 6: **Climate change will impact each species' movement rates differently, but changes will also vary spatially.** The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values  $< 1$  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). The predictions only account for the predicted temperature throughout the areas and ignore environmental factors such as terrain slope, soil type, and forest density. All maps are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

353 change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall,  
 354 RSS decreased throughout most of each species' current range, although elk, cougars, and  
 355 bears were predicted to increase their selection for higher-altitude habitats. Still, none of  
 356 the species were projected to increase RSS throughout their habitat (9).

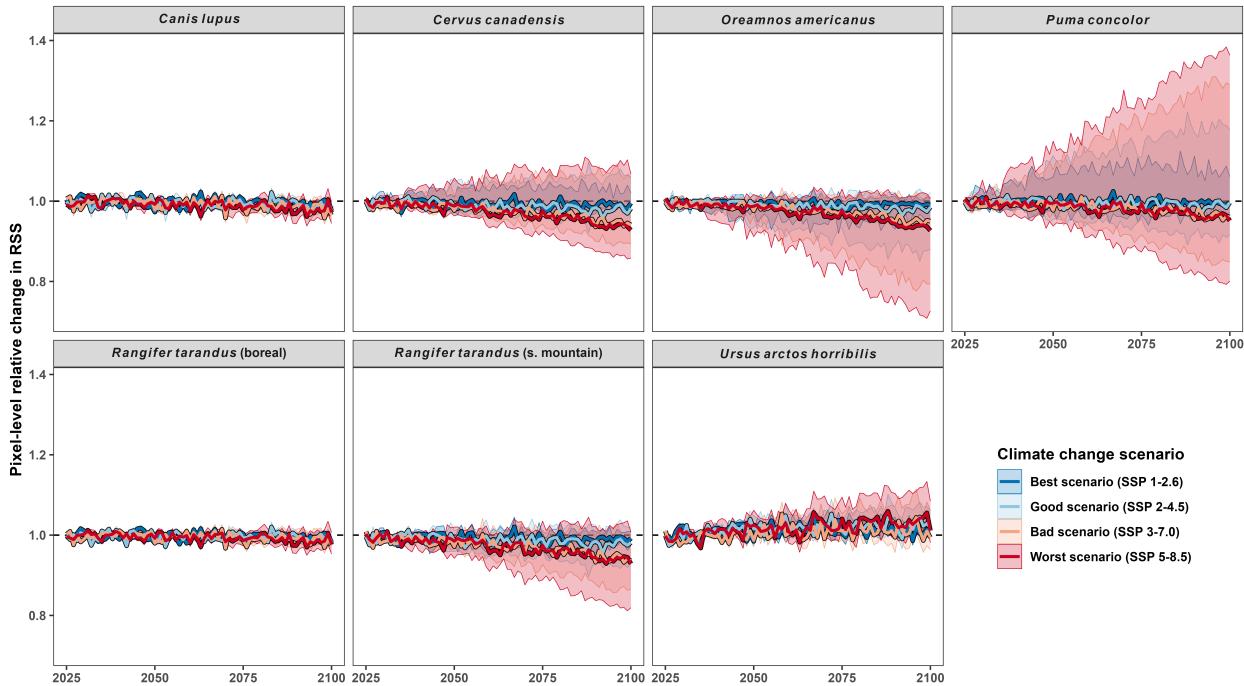
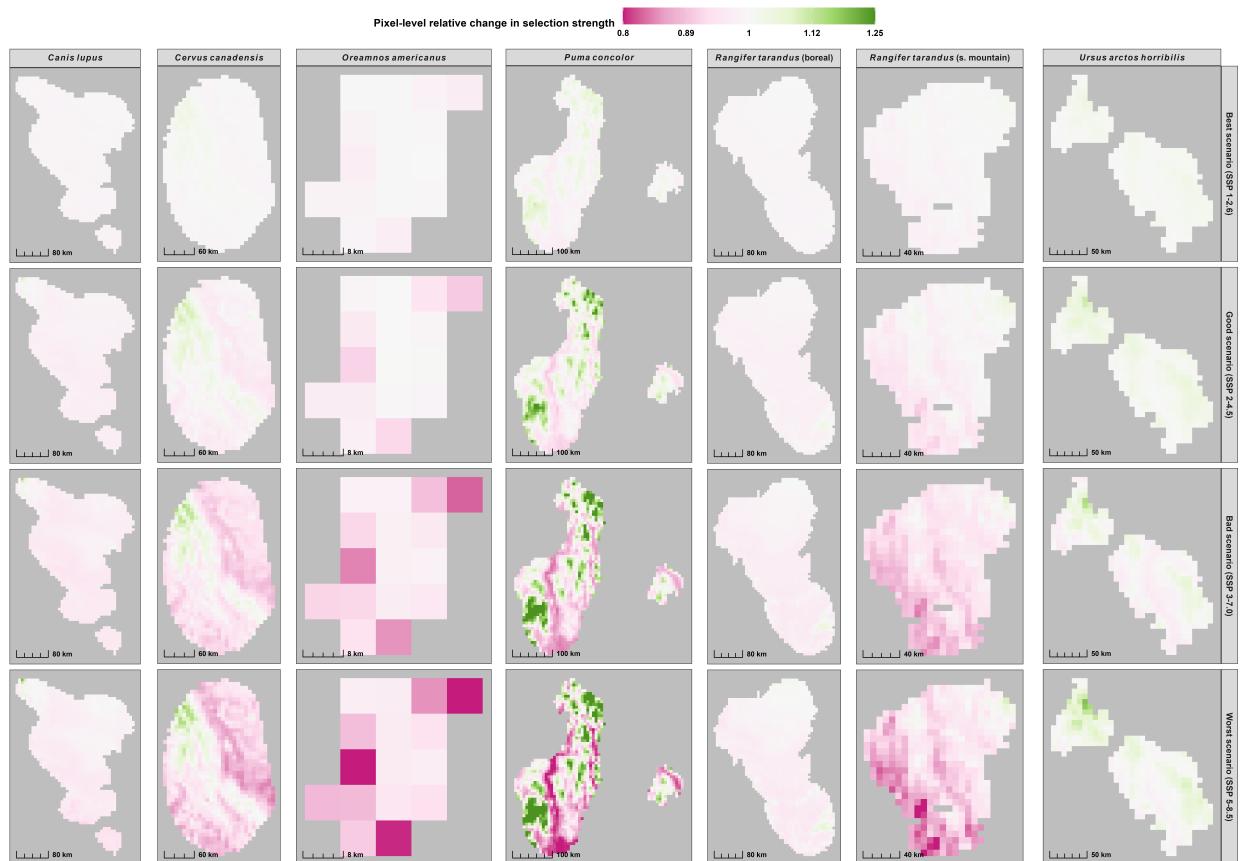


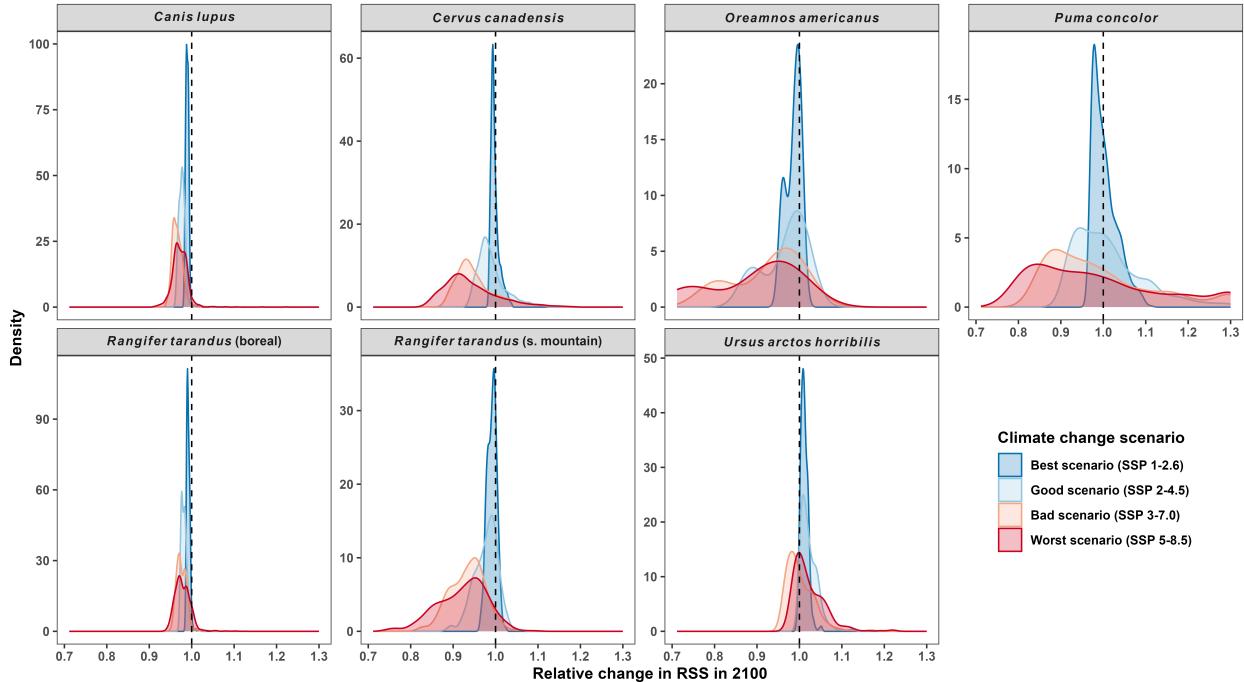
Figure 7: Species will adapt their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas indicate the 95<sup>th</sup> and 5<sup>th</sup> percentiles in change in RSS. Values > 1 indicate an increase, while values < 1 indicate a decrease. Changes are relative to each location's mean RSS in 2025, averaged across the four Shared Socioeconomic Pathways (SSPs).

## 357 4 Discussion

358 We have demonstrated that temperature is an important determinant of how and where  
 359 large mammals move, and that mammals alter their seasonal and daily cycles in movement  
 360 behavior in response to changes in temperature. Predicting mammals' responses to climate  
 361 change remains a challenge, as habitats warm rapidly and mammals are exposed to increas-  
 362 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,  
 363 2023). We leveraged the flexibility and interpretability of GAMs to estimate the (nonlinear)  
 364 responses of terrestrial mammals to temperature. In particular, tensor product interaction



**Figure 8: Climate change will impact each species' 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 0.8 and 1.25 ( $\approx 2^{\pm 0.322}$ ; original data ranged 0.71 to 1.93). All maps are shown in the BC Albers Equal Area Conic projection (EPSG:3005).



**Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact.** The density plots indicate each species' change in RSS in 2100 for their current habitat (Fig. 8), relative to each location's RSS in 2025. Values < 1 indicate a decrease and values > 1 indicate an increase. For ease of readability, values > 1.3 were changed to 1.3 (original maximum: 1.93).

365 terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends  
 366 with temperature. By allowing interaction terms to be smooth bivariate functions, we were  
 367 able to quantify changes in movement behavior without the need to discretize time into  
 368 distinct windows (e.g., day/night and seasons). We were thus able to present changes using  
 369 relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed detailed and  
 370 nuanced estimates of change. This framework was essential for estimating how mammals  
 371 behave in extreme conditions for which data are scarce.

372 As temperatures warm, mammals' risk of hyperthermia increases nonlinearly (Sherwood  
 373 & Huber, 2010), especially for large-bodied species (Alston *et al.*, 2020; Dyer *et al.*, 2023;  
 374 Verzuh *et al.*, 2023). The recent increase in frequency and duration of extreme-temperature  
 375 events (Bunnell *et al.*, 2011; Kienzle, 2018; Yao *et al.*, 2022; IPCC, 2023; Zhang *et al.*, 2023)  
 376 have forced many mammals towards increasingly atypical behaviours with long-term conse-  
 377 quences, ranging from changes in the behavior and fitness of individuals (Cunningham *et al.*,  
 378 2021; Brivio *et al.*, 2024) to mass die-offs (Ameca y Juárez *et al.*, 2012). A species' ability

379 to respond to changing temperature and phenology depends mainly on the its exposure,  
380 sensitivity, and adaptability to changes, and growing evidence suggests that many mammals  
381 in western Canada will struggle to respond due limitations in all three factors (Ameca y  
382 Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Firstly, exposure to warming temperatures  
383 is widespread throughout the area, and warming is expected to accelerate over the coming  
384 decades (Bunnell *et al.*, 2011; Diffenbaugh & Field, 2013; Kienzle, 2018; Eum *et al.*, 2023;  
385 IPCC, 2023). Secondly, large-bodied mammals are particularly sensitive to high heat (Dyer  
386 *et al.*, 2023), but small-bodied mammals are also affected (Krebs *et al.*, 2019; Ratnayake  
387 *et al.*, 2019). Finally, species' adaptability is tested by the speed of climate change (Diff-  
388 enbaugh & Field, 2013) and the rigidity of many speices' photoperiod-dependent phenology  
389 (Walker *et al.*, 2019).

390 Our results suggest that climate change will cause mammals to alter their seasonal move-  
391 ment behavior, but not all species will respond similarly. For example, hotter temperatures  
392 caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-  
393 mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*  
394 *al.* (2025). The increase in movement rates during the colder seasons are likely partly due  
395 to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising  
396 temperatures during snowy seasons also increase the chances of rain-on-snow events, which  
397 limit forage availability and increase the ungulates' need to search for food (Stien *et al.*,  
398 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). In contrast, the reduced movement rates  
399 during warmer summers are likely mainly due to caribou searching for shelter from the heat  
400 due to ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023).  
401 The effects of extreme temperatures are exacerbated by phenological mismatches with sea-  
402 sonal photoperiod (Walker *et al.*, 2019), including the timing of molting and reproduction.  
403 Earlier growth seasons in boreal and arctic regions have resulted in lower calf birth and sur-  
404 vival (Post & Forchhammer, 2008), while the lengthening of the growth season has allowed  
405 moose (*Alces alces*) and deer (*Odocoileus* spp.) to encroach on boreal caribou habitat, along

406 with increased density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;  
407 DeMars *et al.*, 2023). Thus, rising temperatures affect more than each individual species'  
408 movement behavior; they have complex and interconnected effects on an entire community  
409 and its trophic structure.

410 Our results suggest that rising temperatures will have similar effects on boreal wolves.  
411 Warmer temperatures caused wolves to travel further throughout the year, but, similarly  
412 to boreal caribou, they moved substantially less at temperatures above 25°C in summer.  
413 At temperatures above 20°, both boreal caribou and wolves tended to move less during the  
414 day and more between 17:00 and 24:00. This synchronicity in movement patterns is likely  
415 to increase encounters between the two species, particularly when coupled with increasing  
416 human disturbances, since wolves leverage seismic lines and other anthropogenic linear fea-  
417 tures (e.g., roads) to reduce movement costs while increasing the chances of encountering  
418 prey (Whittington *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*, 2022). Additionally, caribou  
419 that attempt to reduce predation risk from wolves by avoiding wolf habitat may risk increas-  
420 ing predation pressure from bears (Leblond *et al.*, 2016) and other encroaching predators  
421 (DeMars *et al.*, 2023). As temperatures rise and allow new competitors and predators to  
422 encroach on boreal caribou habitat (Barber *et al.*, 2018; DeMars *et al.*, 2023; Labadie *et al.*,  
423 2023), climate change will have complex consequences not only for individual species but for  
424 entire communities and their trophic interactions.

425 Considerations about changes in trophic interactions leads to an important caveat about  
426 the results we present. The estimated effects of temperature on movement behavior cannot  
427 be fully attributed to physiological responses to changes in temperature alone, since other  
428 aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For  
429 example, mountain goats' reduced movement rates at temperatures near 0°C in winter may  
430 be due to increased movement difficulty, since melting snow and rain-on-snow events affect  
431 the energetic costs of movement (White, 2025) and encounter rates with predators (Sullender  
432 *et al.*, 2023). However, milder temperatures can also increase plant growth, which, in turn,

allows goats to spend less time searching for forage (White *et al.*, 2025). Therefore, the figure 3 illustrates an estimate of the total effect of temperature on each species movement rates, but it does not explicitly account for energetic costs. Similarly, species' changes in habitat selection do not explicitly account for any changes in physiological or energetic costs. Both mountain goats and elk selected for higher elevation as temperatures warmed, but our models did not explicitly account for differences in forage availability at different altitudes.

Forage quality and availability is often a limiting factor for mammals' ability to adapt to warming temperatures by moving to higher altitudes. Plants are slower to arrive in and establish in new habitats than mammals, and the advance of herbivores can further limit plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh & Field, 2013). Consequently, mammals that move to higher elevations may be forced to spend more time foraging (Mezzini *et al.*, 2025), which will increase their energetic expenditure as well as their chances of encountering predators (including cougars and grizzly bears) or competitors (Kohl *et al.*, 2019; Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). Additionally, plants at high elevations may have weaker defenses against herbivory and be more susceptible to overgrazing (Callis-Duehl *et al.*, 2017). The scarcity and susceptibility of forage may thus limit herbivores' ability to shift elevationally, particularly if predation rates remain relatively unchanged or increase. Furthermore, the physical upper limit to elevation can cause individuals to become trapped. If local peaks become unsuitable habitat, and moving to nearby higher peaks requires traveling across low-quality and high-risk habitat (Figure 8), habitat fragmentation may become too excessive to move across patches or alternative ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may help avoid such a scenario, but the success of relocations can be highly species-dependent, and attempts are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

Changes in mammals' seasonal movement behavior are also likely to affect the timing and frequency of human-wildlife interactions. Since heat affects mammals' sleep quality and likelihood to enter torpor (Fjelldal *et al.*, 2021; Wells *et al.*, 2022; Mortlock *et al.*, 2024),

460 future decades may see increased levels of incidents with bears that struggle to enter or  
461 remain in hibernation (Johnson *et al.*, 2018). The risk is further increased when bears' are  
462 unable to meet their increased energetic requirements through foraging or hunting. Projected  
463 increases in park attendance due to rising temperatures and human population density in  
464 Western Canada are expected to further increase frequency of human-wildlife interactions  
465 (Weststrate *et al.*, 2024).

#### 466 4.1 Consequences for conservation

467 Species' adaptability to rising temperatures is challenged by the aforementioned simulta-  
468 neous, multifarious, and interconnected stressors caused by climate change, since responding  
469 to many concurrent changes at once is particularly difficult (Diffenbaugh & Field, 2013;  
470 Polazzo *et al.*, 2024). Locations may thus not be able to support species and population  
471 sizes they supported historically, and species may thus not select for historical geographical  
472 ranges in the future. It is therefore crucial for conservationists and other decision-makers  
473 to distinguish between a species' ideal environmental space (or E space, *sensu* Matthiopoulos,  
474 2022), and its best available geographic space (or G space, *sensu* Matthiopoulos, 2022).  
475 Accelerating multifarious change in species' movement behavior and energetic costs require  
476 conservation measures to be proactive and anticipate future changes, even when future con-  
477 ditions are substantially different from historical conditions and historical data may not be  
478 available. To this end, the framework presented by Polazzo *et al.* (2024) for estimating  
479 species' responses to multifarious change becomes essential, particularly when accounting  
480 for energetic and fitness costs, as argued by Cunningham *et al.* (2021).

481 As of December 2024, only 13.8% of terrestrial Canada was within protected areas or  
482 other conserved areas (Environment and Climate Change Canada, 2025), so rapid action  
483 is necessary to protect additional 16.2% of Canada's land by 2030 in accordance with  
484 Kunming-Montreal Global Biodiversity Framework (i.e., the "30 by 30 initiative"; Conven-  
485 tion on Biological Diversity, 2022). However, the choice of what habitats to protect will re-

486 quire careful consideration, since protected areas should support species not only in present  
487 conditions but also as species' needs and selection change over the coming decades (Simmons  
488 *et al.*, 2021). As anthropogenic activity increasingly alters habitats and community struc-  
489 tures (Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022), protecting  
490 biodiversity and the habitats it depends on will require widespread and collaboration with  
491 local stakeholders, especially Indigenous Peoples, to ensure that all decisions are culturally  
492 sound and respect Treaties (Turner & Clifton, 2009; Desjardins *et al.*, 2020; Wong *et al.*,  
493 2020; Hessami *et al.*, 2021; Falardeau *et al.*, 2022; Lamb *et al.*, 2023). Understanding the  
494 consequences of climate change in mammalian movement behaviour is a first step towards  
495 proactively responding to how mammals will respond to human-induced rapid environmental  
496 change (Sih *et al.*, 2011; Williams & Blois, 2018). However, a better understanding of such  
497 consequences will require a more holistic approach that includes carefully data collection,  
498 model design, and interpretation and application of results.

499 **4.2 Study limitations and considerations for future work**

500 ***HERE***

501 Estimated selection strength for forest cover was weak and did not change strongly with  
502 temperature. Time-varying rasters of forest cover would have likely given stronger (and  
503 better) estimates.

- 504 • variation among individuals: Jeltsch *et al.* (2025). Population-level means that ignore  
505 such variation can greatly limit the efficacy of conservation projects (Muff *et al.*, 2020;  
506 Mortlock *et al.*, 2024; Silva *et al.*, 2025).
- 507 • we see clear signals despite the data issues and limitations, but more work needs to be  
508 done to disentangle important drivers

509 More work is necessary on quantifying interspecific responses to temperature, including  
510 the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et*

511 *al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events  
512 (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of  
513 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;  
514 Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at  
515 the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially  
516 since landscape changes will likely depend not only on the direct effect of temperature but  
517 also on cascading changes in the availability and unpredictability of resources (McLellan &  
518 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

519 Future work should explore the effects of temperature on movement behaviour while  
520 accounting for finer-scale and species specific variables that were not accounted for in this  
521 study. Examples of these include temporally dynamic measures of forest type and age, canopy  
522 density, competitive pressures, forage availability, and predator avoidance, or environmental  
523 stochasticity. However, many of these data not available, so we also suggest that more  
524 work be done on quantifying such measures using spatiotemporally dynamic models and  
525 sufficiently fine resolutions. ... animals in the study are generalists; we need more work on  
526 specialists and smaller species, but they can be harder to track

527 changes in the phenology of plants, fire, ice, or mammalian physiology (e.g., moulting,  
528 fat storages) or behaviour (e.g., migration, food caching), other than as direct responses to  
529 temperature.

- 530 • other confounding causes of movement (forest age, structure, fire, type, dist\_water,  
531 etc.) change over the years but are assumed to be fixed
- 532 • the temporal resolution of climate change projections isn't great (many steps necessary  
533 to simulate weather)

534 ***old text:***

535 Our work highlights three central considerations for future research: (1) telemetry sam-  
536 pling 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 duration of each telemetry should depend not just on population size but also the (accelerating) rate of environmental change, and (3) predicting changes in movement behaviour becomes highly complex when responses are nonlinear, especially when changes depend on many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

While the `ctmm` movement models produced scale-independent estimates of speed (i.e., model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accuracy, size, and stability of speed estimates still depended on the GPS sampling frequency. This dependency is because coarsely-sampled movement data contains information on large-scale movements (range crossings, migrations) but not fine-scale movements (Noonan *et al.*, 2019a; Nathan *et al.*, 2022), including first-order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour sampling interval allows us to reasonably estimate the caribou's movement path at a temporal scale of approximately 13 hours (or greater), but we cannot produce reasonable movement trajectories at a much finer (e.g., hourly) scale. Consequently, we suggest being cautious when comparing estimated movement behaviours across species, even though all predictions have been corrected to the hourly timescale by predicting for 1-hour time intervals. Ideally, sampling schedules should be fine enough to reconstruct individuals' movement paths. ***make data useful for future studies. recognize cost of GPS and suggest IoT (Wild et al., 2023), although station coverage can be a limitation (denicola\_monitoring\_2025?).*** Good estimates of an animal's speed and trajectory require telemetry locations to be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so that, on average, the dataset contains multiple locations in between changes in direction. What constitutes a change in direction depends on what movement scale one is investigating. Small-scale movements and first-order spatial selection will require more frequent sampling than migratory movement

564 or second-order and third-order spatial selection. While `ctmm` movement models are scale-  
565 invariant in that any model can be scaled to larger or smaller areas and timescales (Noonan  
566 *et al.*, 2019a), the model estimates are not independent of the scale of the sampling frequency  
567 (DeNicola *et al.*, 2025). When tracking data are too coarse for accurate speed estimation,  
568 diffusion rates (measured in area per unit time) may be a useful alternative for quantifying  
569 animals' exploration rates (DeNicola *et al.*, 2025). ***also need better way to distinguish***  
570 ***between sates. HMMs are an option, but there are limitations.***

## 571 Other refs and miscellaneous maerial

572 GAMs' flexibility and complexity can also be a frustrating limitation if used too gener-  
573 ously. As such, analysts should chose the basis size for each smooth term carefully. While  
574 penalized splines and REML can help avoid unruly smooth terms that would result in ques-  
575 tionable estimates where data are scarce (Wood, 2017), it is best to select the basis size  
576 of the smooth terms with parsimony, especially when datasets are large. Still, predicting  
577 mammals' responses at the data-scarce fringes of the surface plots in Figs. 3 and 4 comes  
578 with greater uncertainty, particularly given that the changes are nonlinear.

## 579 5 Author contributions

580 SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote  
581 code for estimating instantaneous movement speeds. MJN conceived of the project idea and  
582 supervised SM throughout the project. All other authors, which are listed in alphabetical  
583 order by last name, contributed telemetry data and reviewed the interpretation of the results  
584 for their species of interest. All authors contributed to reviewing the manuscript.

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