

# 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 and phenology in the 21<sup>st</sup> century. We address this gap by using 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 significantly affects 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. However, species did not respond uniformly to rising temperatures, so community-level responses will likely be complex, as climate change will cause species to alter their seasonal movement behavior and increase their chances of hyperthermia. Median habitat selection strength decreased for most 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 they begin to select against their current ranges. As climate change exposes mammals to novel environmental conditions, proactively predicting changes in mammalian movement behaviour will become crucial for effectively and proactively understanding community-level responses 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.

## <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 by moving to thermal refugia (Hannah *et al.*, 2014;  
<sup>12</sup> Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022),  
<sup>13</sup> which 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 am-

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

In the last century, many ecosystems experienced widespread warming that resulted in milder and shorter winters, hotter and longer summers, and a greater risk of extremely high temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and fragmentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear how or whether species will be able to respond to climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and responding to future changes require a detailed understanding of how temperature will affect how and where different mammalian species move (Cunningham *et al.*, 2021). Recent work has documented the effects of climate change on mammals’ ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and movement behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023). However, there remains a need for fine-scale

54 estimates of the effects of temperature on mammals' movement behaviour and quantitative  
55 predictions of changes in movement behaviour with climate change in the current century  
56 (IPCC, 2023).

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

73 Large-bodied mammals are most likely to show changes in movement behaviour with  
74 rising temperatures, since they tend to move long distances (Merkle *et al.*, 2016), are partic-  
75 ularly sensitive to overheating (Fuller *et al.*, 2016), and their movement rates are thus strongly  
76 limited by excessive heat (Dyer *et al.*, 2023). Conveniently, their large body size also allows  
77 for larger tracking devices that have longer battery life and allow longer tracking periods  
78 and with finer temporal resolution (Kenward, 2001). In this paper, we quantify the effects of  
79 proximal air temperature on mammalian movement behaviour, namely movement rates and  
80 habitat selection of six large-bodied terrestrial mammal species in western Canada (boreal

and southern mountain caribou: *Rangifer tarandus*, cougars: *Puma concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*, mountain goats: *Oreamnos americanus*, and wolves: *Canis lupus*; Table 1). Using over 25 years of telemetry data throughout a large spatial range of western Canada and hourly air temperature data, we estimate how these mammals altered their probability of moving, speed when moving, and habitat selection in response to temperature. We then pair the estimated responses with monthly climate change projections (Mahony *et al.*, 2022) to forecast each species' movement behaviour during the 21<sup>st</sup> century under four different climate-change scenarios, namely Shared Socioeconomic Pathways (SSPs): 1-2.6 ("Sustainability – Taking the Green Road"; low challenges to mitigation and adaptation), 2-4.5 ("Middle of the Road: medium challenges to mitigation and adaptation), 3-7.0 ("Regional Rivalry – A Rocky Road"; high challenges to mitigation and adaptation), and 5-8.5 ("Fossil-fueled Development – Taking the Highway"; high challenges to mitigation, low challenges to adaptation). Riahi *et al.* (2017) provide a detailed overview of SSPs. We discuss the consequences of these changes in movement behaviour at the individual, population, and community levels. We also provide directions for future research and solutions for overcoming some common data limitations.

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

Species	Start	End	n	$\Delta t$ (hours)	Animals	Has speed
Caribou (boreal)	2011-03-02	2018-01-03	200,561	13.00	146	131
Caribou (southern mountain)	1998-03-20	2009-06-06	27,921	6.00	22	20
Cougars	2006-02-04	2021-07-12	80,650	2.00	29	29
Elk	2007-01-13	2013-11-19	875,853	2.00	169	169
Grizzly bears	2004-09-29	2009-09-07	39,021	1.00	18	18
Mountain goats	2019-06-24	2023-10-04	65,452	6.25	11	10
Wolves	2013-01-26	2017-08-29	202,433	0.25	39	39

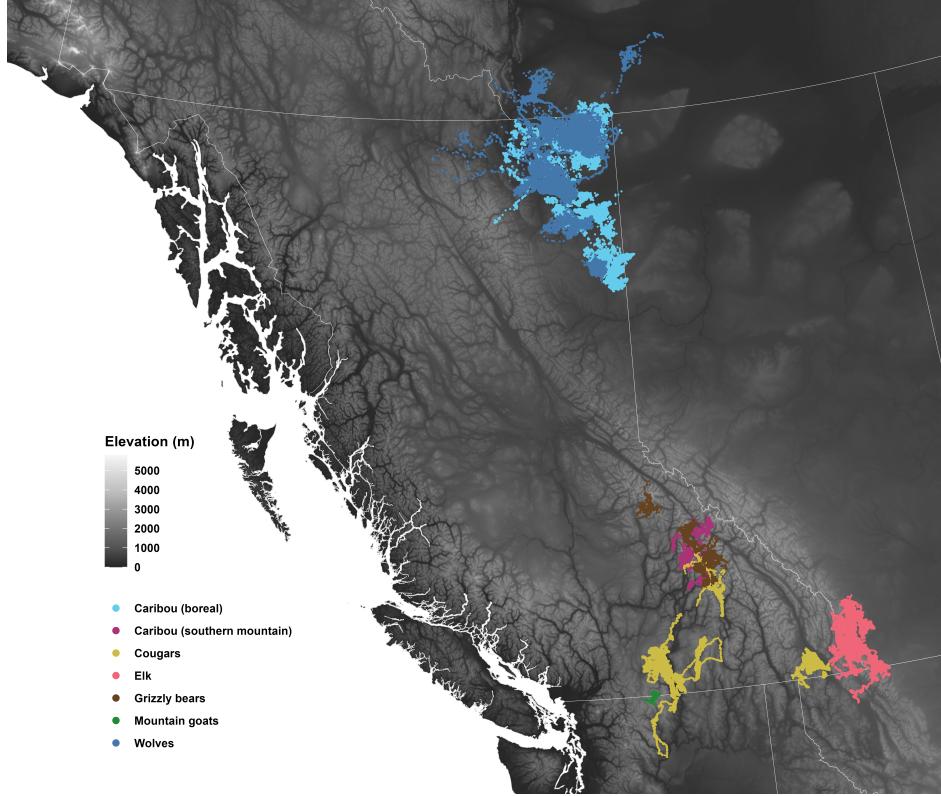


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

## 97 2 Methods

### 98 2.1 Datasets used

99 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry  
 100 data (Fig. 1); (2) historical hourly air temperature from the ERA5 reanalyzed dataset (Euro-  
 101 pean Center for Medium-range Weather Forecasting; Hersbach *et al.*, 2023); (3) temporally  
 102 static rasters of percent forest cover, elevation, and distance from water; and (4) climate  
 103 change projections under four Shared Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017).

104 While we acknowledge there are other important variables (e.g., forest type, structure, and  
 105 age; terrain slope and aspect), we limited our models to only use three simple variables for  
 106 the sake of parsimony and comparability across species. The simplicity of the models also  
 107 allowed for simple forecasts under the assumption of temporally invariant landscapes. See  
 108 the discussion section for additional detail on the advantages and limitations of using such

109 simple models.

110 **2.1.1 GPS telemetry data**

111 Boreal caribou and wolf telemetries were acquired from a data repository of the British  
112 Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected  
113 as part of the boreal caribou radio-collaring program of the BC OGRIS Research and Ef-  
114 fectiveness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data  
115 **XXX**. Cougar data include telemetries from Darlington *et al.* (2025) and (**serrouya\_ref?**).  
116 Elk data from the work of Ciuti *et al.* (2012) were downloaded from Movebank (Kays *et*  
117 *al.*, 2022). **MISSING INFO ON GRIZZLY BEAR AND GOAT TELEMETRY**

118 **DATA.**

119 From the full set of telemetry data, we removed a total of 2396 problematic GPS locations  
120 (0.16%, including collar calibration data) after inspecting diagnostic plots of (1) distance  
121 from the median location, (2) straight-line displacement between locations, (3) turning angle,  
122 and (4) time interval between consecutive points. Particular attention was paid to points  
123 with large turning angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially  
124 if antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

125 **2.1.2 Historical temperature data and climate change projections**

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

132 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA (v.  
133 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly tempera-

tures from 2025 to 2100 at a  $0.08^\circ$  spatial resolution. Since the climate projections only provided monthly means and ranges but no measures of variance or distributional assumptions, we used the historical data for western Canada from 1998 to 2023 (extremes included) to estimate the monthly variation in temperature, which we defined as  $\sigma_T^2$ , the variance at location  $\langle x, y \rangle$  in month  $m$  for each year (e.g., the variance at coordinates  $\langle -119.40, 49.94 \rangle$  in April 2005). We then modeled the estimated variance using a Generalized Additive Model (GAM) for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017) using the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear predictor for the location (i.e., the mean) included smooth terms of: each year's estimated within-pixel monthly mean temperature ( $\hat{\mu}_T$ ), month ( $m$ ), a two-dimensional smooth of spatial coordinates  $\langle x, y \rangle$ , and a tensor product interaction term of month and space to allow for seasonal terms to vary smoothly over space. The linear predictor for the scale term, which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included smooth terms of the monthly mean temperature, month, and space. We did not include smooth terms of year to avoid unrealistic projections when extrapolating beyond past 2023.

The model was thus

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

where  $\mu_{\sigma_T^2}$  and  $\nu_{\sigma_T^2}$  indicate the location and scale parameters of the gamma distribution of  $\sigma_T^2$ , and together they determine the variance of  $\sigma_T^2$ , indicated as  $\mathbb{V}(\sigma_T^2)$ . Functions  $f_{L,j}$  and  $f_{S,j}$  indicate the  $j^{\text{th}}$  smooth functions for the location and scale parameters, respectively. To ensure the smooth functions of month,  $f_{L,2}(m)$  and  $f_{S,2}(m)$ , joined smoothly between

154 December and January, the terms use cyclic cubic spline bases. The spatial terms used two-  
155 dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood  
156 (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood  
157 (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information  
158 on the code used to fit the model.

159 We simulated hourly variation in future years by assuming hourly temperature followed  
160 a normal distribution with mean specified by the monthly `climatenar` climate projections  
161 and variance as specified by the gamma GMLS. For each month within each year from  
162 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the  
163 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the  
164 (normalized) Gaussian probability density for each quantile.

### 165 2.1.3 Resource rasters

166 We estimated percent forest cover and distance from water using the temporally static  
167 rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing  
168 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-  
169 ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted  
170 the raster of percent cover of open water (class 12) to a binary raster of pixels with water  
171 ( $\text{cover} > 0\%$ ) or without water ( $\text{cover} = 0\%$ ) and then calculated each pixel's distance from  
172 the nearest pixel with water using the `distance()` function from the `terra` package. Fi-  
173 nally, we obtained two digital elevation models using the `get_elev_raster()` function from  
174 the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6  
175 (a resolution of  $0.009^\circ$ ) for model fitting and one with a zoom of 3 (a resolution of  $0.08^\circ$ )  
176 for downloading climate change projections via `climatenar`. All final rasters and code are  
177 available on GitHub (see the Data Availability Statement). For ease of interpretability and  
178 comparison with current conditions, we assumed resources would remain constant through  
179 to 2100, although we recognize that the spatial distribution of forest cover and open water

180 will likely change throughout the 21<sup>st</sup> century.

181 **2.2 Estimating mammals' instantaneous speeds**

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

189 Since `ctmm`'s movement models assume a single moving state with stochastic but non-zero  
190 speed (Calabrese *et al.*, 2016; Noonan *et al.*, 2019a), we corrected data-informed speeds so  
191 that the minimum instantaneous speed could be 0. We performed this correction by sub-  
192 tracting each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function  
193 we used is available on GitHub (see the Data Availability Statement). To avoid artifacts  
194 due to excessively small, non-zero speeds, we determined whether an animal was moving or  
195 not using a  $k$ -means algorithm with 2 clusters for each species' distribution of detrended  
196 speeds. When the algorithm clearly failed to discriminate between states, we estimated the  
197 split point using the inflection points in histograms of the detrended speeds (Fig. B1).

198 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

199 Ambient temperature is only one of the many drivers of mammalian movement behaviour  
200 (Fig. 2). Many species alter their movement rates (e.g., movement frequency and speed)  
201 daily or seasonally in response to factors such as solar time, photoperiod, forage availability,  
202 reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates  
203 throughout the day and across seasons. Therefore, estimating the effects of temperature  
204 on movement rates requires accounting for how mammals' response to temperature changes

with time of day and day of year (Fig. 2A; Péron *et al.*, 2017; Buderman *et al.*, 2018; Leclerc *et al.*, 2021; Xu *et al.*, 2021). Similarly, mammals' selection strength for resources depends on ambient temperature, since higher temperatures can promote a selection for refuge from heat (e.g., thicker forest cover, higher elevation, proximity to water; Attias *et al.*, 2018; Giroux *et al.*, 2023).

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

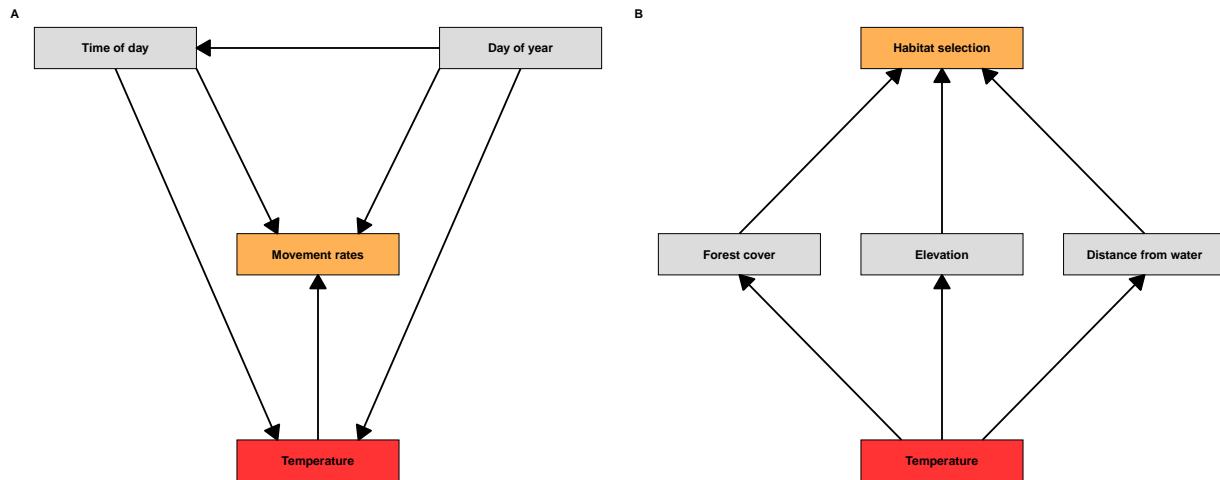


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time 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.

217 **2.3.1 Effects of temperature on movement rates**

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

229 The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species  
230 ( $\beta_s$ ), random intercepts for each animal ( $Z_a$ ), and species-level `by` smooths that allowed  
231 independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*  
232 *al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific Daylight Time;  
233 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time  
234 of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017).  
235 The models also had three tensor product interaction terms `by` each species: (1) day of year  
236 and time of day, (2) temperature and time of day, and (3) temperature and day of year.  
237 These three terms accounted for smooth changes in: (1) daily behaviour across day of year,  
238 (2) the response to temperature over time of day (e.g., changes in nocturnality), and (3)  
239 the response to temperature over day of year (e.g., the timing of molting, migration, and  
240 hibernation). Finally, two smooth terms of log-transformed sampling interval (`dt`; hours)  
241 corrected for biases in speed estimates arising from irregular GPS sampling intervals, since  
242 longer intervals result in lower speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025).  
243 A global smooth term of `log(dt)` accounted for the overall effect of sampling interval, while

244 a factor-smooth interaction term (`bs = 'fs'`) of  $\log(\text{dt})$  and species-  
 245 level deviations from the global term while assuming a common smoothness parameter across  
 246 species (model GS in Figure 4 of Pedersen *et al.*, 2019). Formally, the model for movement  
 247 state  $M$ , with  $M = 0$  indicating no movement and  $M = 1$  indicating movement, was

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

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

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

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

253 **2.3.2 Effects of temperature on habitat selection**

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

266 Each species' model had the same structure:

$$\left\{ \begin{array}{l} O \sim \text{Pois}(\lambda) \\ \mathbb{E}(O) = \mathbb{V}(O) = \lambda \\ \log(\lambda) = f_1(\text{forest\_perc}) + f_2(\text{elevation\_m}) + f_3(\text{dist\_water\_m}) + \\ Z_a + f_{4,a}(\text{forest\_perc}) + f_{5,a}(\text{elevation\_m}) + f_{6,a}(\text{dist\_water\_m}) + \\ f_7(\text{forest\_perc}, \text{temp\_c}) + f_8(\text{elevation\_m}, \text{temp\_c}) + \\ f_9(\text{dist\_water\_m}, \text{temp\_c}) + f_{10}(\text{temp\_c}) + f_{11,a}(\text{temp\_c}) \end{array} \right. , \quad (4)$$

267 where  $O$  indicates whether an animal was observed ( $O = 1$ ) or not ( $O = 0$ ), and the  
268 species-level indices are omitted for readability, but each term in the model can be as-  
269 sumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), eleva-  
270 tion (`elevation_m`, in meters), and distance to water (`dist_water_m`, in meters) accounted

for the species-level selection strength for each resource. A Gaussian random effect for each individual animal ( $Z_a$ ) corrected for uneven sampling across individuals, while factor-smooth interaction terms for each animal ( $f_{j,a}$ ) accounted for animal-level resource selection (i.e., individual-level deviations from the species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction terms of the three resources and temperature (`temp_c`) estimated the smooth change in resource selection at different temperatures. Finally, marginal smooth terms of temperature and factor-smooth interaction terms of temperature and animal accounted for species- and individual-level sampling biases at different temperatures (e.g., sampling more during warm periods).

### 3 Results

Of the GPS fixes with finite speed estimates, 2.6% had temperatures lower than  $-20^{\circ}\text{C}$ , while 6.5% had temperatures above  $20^{\circ}\text{C}$ , and temperature ranges differed across species (Table 2, Fig. B2). Sampling interval affected estimates of probability as well of as speed when moving (Fig. B8). Consequently, we present all results while predicting specifically for one-hour sampling intervals. At  $0^{\circ}\text{C}$ , species differed in estimated mean probabilities of moving ( $\hat{P}(M = 1)$ ; range: 0.05 – 0.31), mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1)$ ; range: 0.42 – 2.67 km/h), and mean distance traveled (i.e.,  $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$ , range: 0.04 – 0.61 km/h; Table 2). Grizzly bears had the lowest movement frequency ( $\hat{P}(M) \approx 0.05$ ), while wolves and cougars moved most often ( $\hat{P}(M) \geq 0.22$ ). Mountain goats and southern mountain caribou moved the slowest ( $\hat{\mathbb{E}}(S|M = 1) \approx 0.43$  km/h), while wolves had the highest mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1) \approx 2.67$  km/h). Consequently, at  $0^{\circ}\text{C}$ , wolves traveled an average of  $0.22 \times 2.67$  km/h  $\approx 0.6$  km/h; 2.5 to 16.7 times further than other species.

Table 2: Summary statistics for each species' GPS fixes with finite speed estimates, namely: the number fixes after data cleaning ( $n$ ), the percentage of fixes with temperature ( $T$ ) below  $-20^{\circ}\text{C}$  and above  $20^{\circ}\text{C}$ , the estimated mean probability of moving ( $\hat{P}(M = 1)$ ), the mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1)$ ; km/h), and the mean distance travelled ( $\hat{P}(M = 1) \times \hat{\mathbb{E}}(S|M = 1) = \hat{\mathbb{E}}(D)$ ; km/h), for a sampling interval of 1 hour and a temperature  $T$  of  $0^{\circ}\text{C}$ .

Species	$n$	$T < -20^{\circ}\text{C}$ (%)	$T > +20^{\circ}\text{C}$ (%)	$\hat{P}(M = 1 T = 0^{\circ}\text{C})$	$\hat{\mathbb{E}}(S M = 1, T = 0^{\circ}\text{C})$	$\hat{\mathbb{E}}(D T = 0^{\circ}\text{C})$
Caribou (boreal)	187,679	6.8	7.9	0.18	0.73	0.13
Caribou (s. mountain)	26,518	1.3	3.4	0.11	0.42	0.05
Cougars	80,621	0.7	6.9	0.31	0.76	0.24
Elk	875,682	2.4	4.9	0.17	0.57	0.10
Grizzly bears	39,001	0.0	8.4	0.05	0.72	0.04
Mountain goats	65,219	0.7	2.8	0.13	0.42	0.06
Wolves	202,386	1.7	13.0	0.22	2.67	0.60
Total	1,477,106	2.6	6.5			

294 Across all species, Relative Selection Strength (RSS) was weakest for forest cover and  
 295 strongest for elevation. At temperatures near  $0^{\circ}\text{C}$ , wolves selected for forest cover ( $\gtrapprox 50\%$ ),  
 296 elevations near 1 km, and distances from water  $< 5$  km; elk selected for intermediate forest  
 297 cover ( $\approx 50\%$ ), elevations between 1 and 2 km, and distances from water of 10-15 km;  
 298 mountain goats selected for sparse forest cover ( $< 25\%$ ), elevations near 1.5 km, and distances  
 299 from water  $< 5$  km; cougars selected for dense forest cover ( $> 75\%$ ), an elevation of  $\sim 1$  km,  
 300 and distances from water  $< 7.5$  km; boreal caribou selected for forest cover between 50% and  
 301 75%, elevations near 500 m, and distances from water  $< 10$  km; southern mountain caribou  
 302 selected for dense forest cover, elevations near 2 km, and distances from water  $\lessapprox 5$  km; and  
 303 grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2  
 304 km, and distances from water  $< 3$  km.

305 There was relatively strong agreement between models with and without temperature  
 306 (Figs. B3, and B14), but including temperature always resulted in better fits (all p-values  
 307  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \leq -342$ ; Appendix B). Accounting for temperature even resulted in  
 308 a simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better  
 309 (lower deviance), and hence no test was necessary to show that the inclusion of temperature

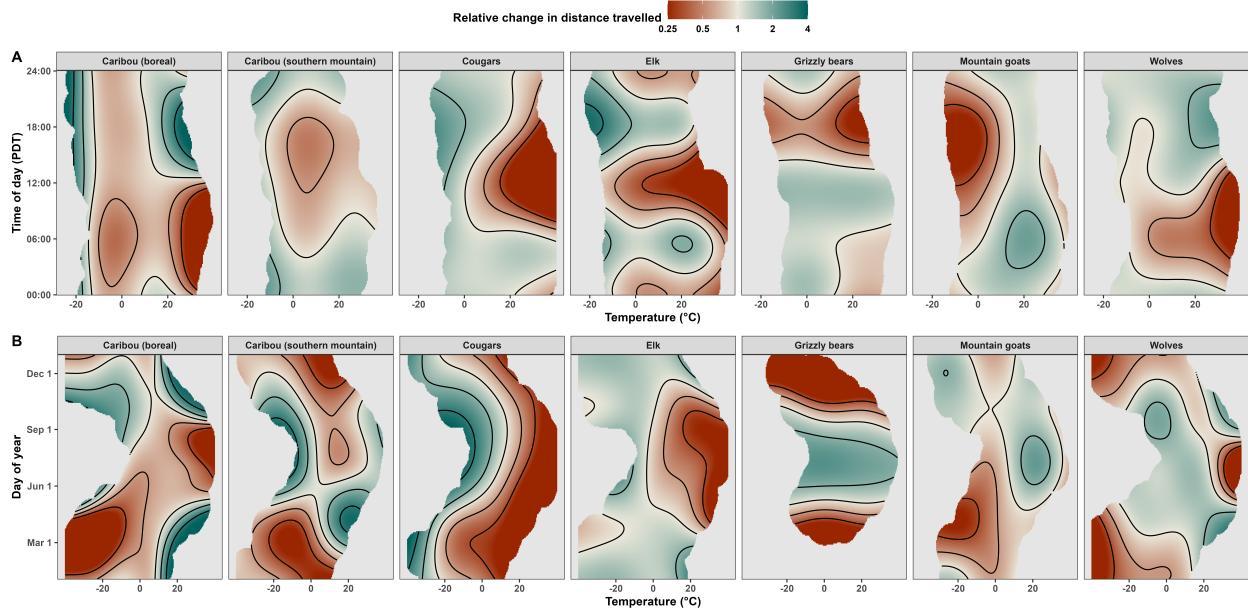
310 produced a better fit.

### 311 3.1 Effects of temperature on movement rates

312 Species' changes in movement rates to temperature varied in both direction and magnitude  
313 (Figs. 3, B4-B6), even after accounting for differences in daily and seasonal activity (e.g.,  
314 sleeping, migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved  
315 and indicated clear shifts in activity over time of day and day of year for all species. The  
316 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions  
317 of the deviance (79.3% for the gamma model and 10.7% for the binomial model, which is  
318 relatively high for a binomial model with binary responses: see ch. 11 of McElreath, 2020).  
319 All species altered their daily and seasonal movement behaviour to changes in temperature  
320 (Fig. 3). The clearest example of this was cougars. In late spring (June 1<sup>st</sup>), they moved  
321 from evening to early morning if temperatures were below 20°C, but if temperatures were  
322 above 20°C they moved mostly between 3:00 and 6:00 AM. Throughout the year, they tended  
323 to move more when it was colder, but what they perceived as "colder" was relative to the  
324 time of year. All species' estimated probability of moving and speed when moving decreased  
325 with sampling intervals above 1 hour, except for cougars' speed, although the estimated  
326 trends were highly uncertain (Fig. B8). Uncertainties around the estimated effects were  
327 generally higher at extreme temperatures due to lower data availability (Figs. B4A, B5A,  
328 and B6A).

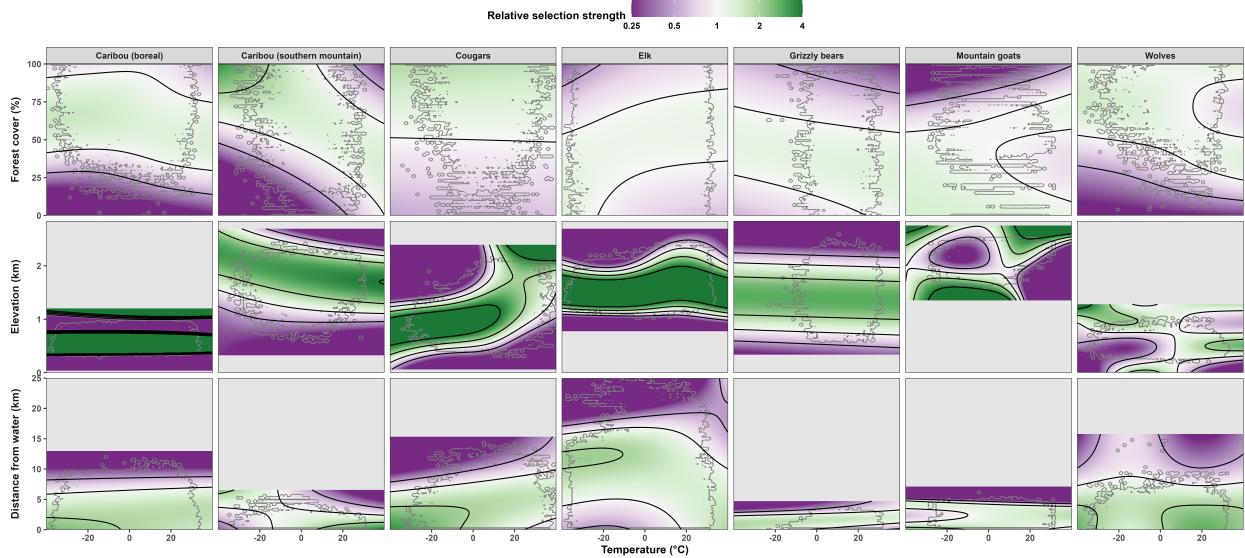
### 329 3.2 Effects of temperature on habitat selection

330 Species' RSS was generally strongest for elevation and weakest for forest cover, but RSS  
331 depended significantly on temperature for all species (all p-values <  $2.2 \times 10^{-16}$ ; Fig. 4).  
332 Changes in RSS with temperature were strongest for elevation and generally weakest for  
333 distance from water, but there were no common trends across all species for any of the  
334 three resources. All species, with the exception of cougars, exhibited clear temperature-



**Figure 3: Temperature is a strong driver 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  $\log_2$  scale to help visualize patterns in doubling, and values are capped to  $2^{\pm 2}$  for ease of readability.

dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed their preference for forested areas, while mountain goats relaxed their preference open areas (cover < 50%). As temperatures warmed, elk and boreal caribou shifted towards more forest cover closer to 50%, while southern mountain caribou and grizzly bears selected for areas with 50% forest cover or less. All species shifted elevationally with temperature, although boreal caribou had a much sharper change in RSS across elevation. Elk, mountain goats, and cougars moved to higher elevations with temperature, while wolves, southern mountain caribou, and grizzly bears moved to lower elevations. 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 km of water. As with movement rates, estimated RSS was generally most uncertain at extreme temperatures, for which data was scarcer (Fig. B15).



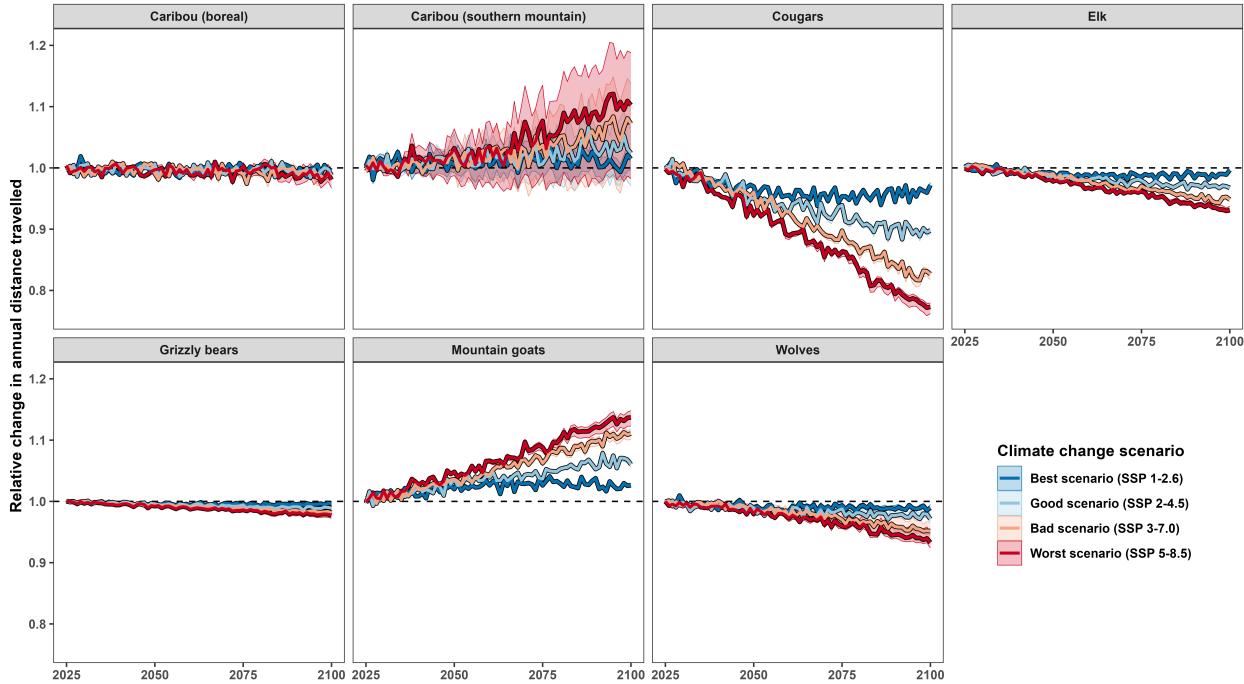
**Figure 4: Mammals’ habitat selection depends on ambient temperature.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species’ observed data. RSS values were re-centered 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). Estimated changes in average distance travelled were negligible for boreal caribou, and grizzly bears, although both species showed seasonal changes in seasonal movement rates. As temperatures warmed, boreal caribou moved further in winter, spring, and fall but less in summer, while grizzly bears showed a clear shift towards earlier emergence from hibernation (Fig. B4) and greater movement earlier in the year but less movement in early fall. Southern mountain caribou and mountain goats are projected to travel further by 2100, although the estimates for southern mountain caribou varied greatly over space (Fig. 6). Cougars, elk, and wolves were projected to move less by 2100, with cougars showing as much as a 24% decrease in mean yearly distance travelled.

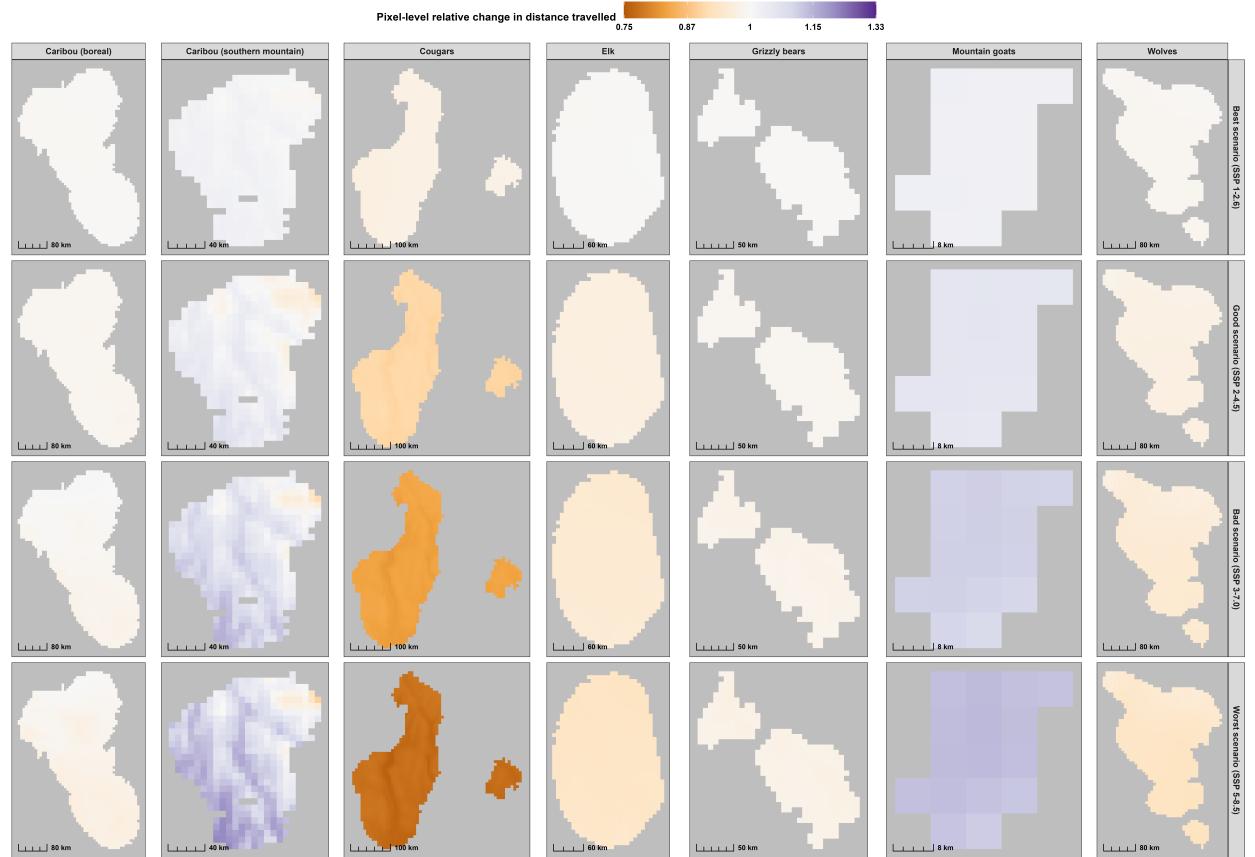
Absolute relative changes in average yearly distance travelled were small under the best-

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). Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change projections (Fig. 6). Again, absolute changes were generally greatest under worse SSPs, but the direction of change at each location also varied across SSPs (most visible in cougars).



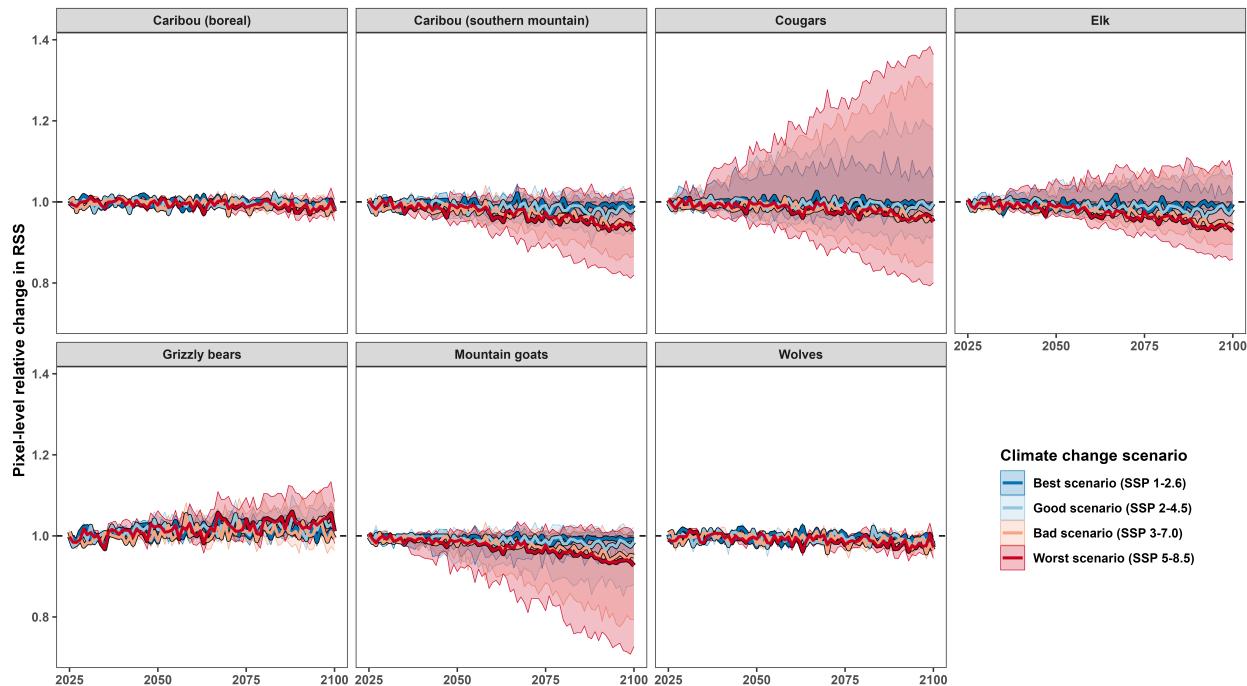
**Figure 5: Species will alter their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change.** Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes 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.

Median RSS was projected to decrease over time within the each species' observed range, but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pronounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and southern mountain caribou. Changes for boreal wolves and caribou were relatively negligible. Elk, cougars, and grizzly bears were predicted to increase their selection strength for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were 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 extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

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



**Figure 7: Species will alter 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).

## 378 4 Discussion

379 We have demonstrated that temperature is an important driver of how and where large mam-  
 380 mals move, and that mammals alter their seasonal and daily cycles in movement behaviour  
 381 in response to changes in temperature. However, predicting mammals' responses to climate  
 382 change remains a challenge, as habitats warm rapidly and mammals are exposed to increas-  
 383 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,  
 384 2023). We leveraged the flexibility and interpretability of GAMs to estimate the (nonlinear)



**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 extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

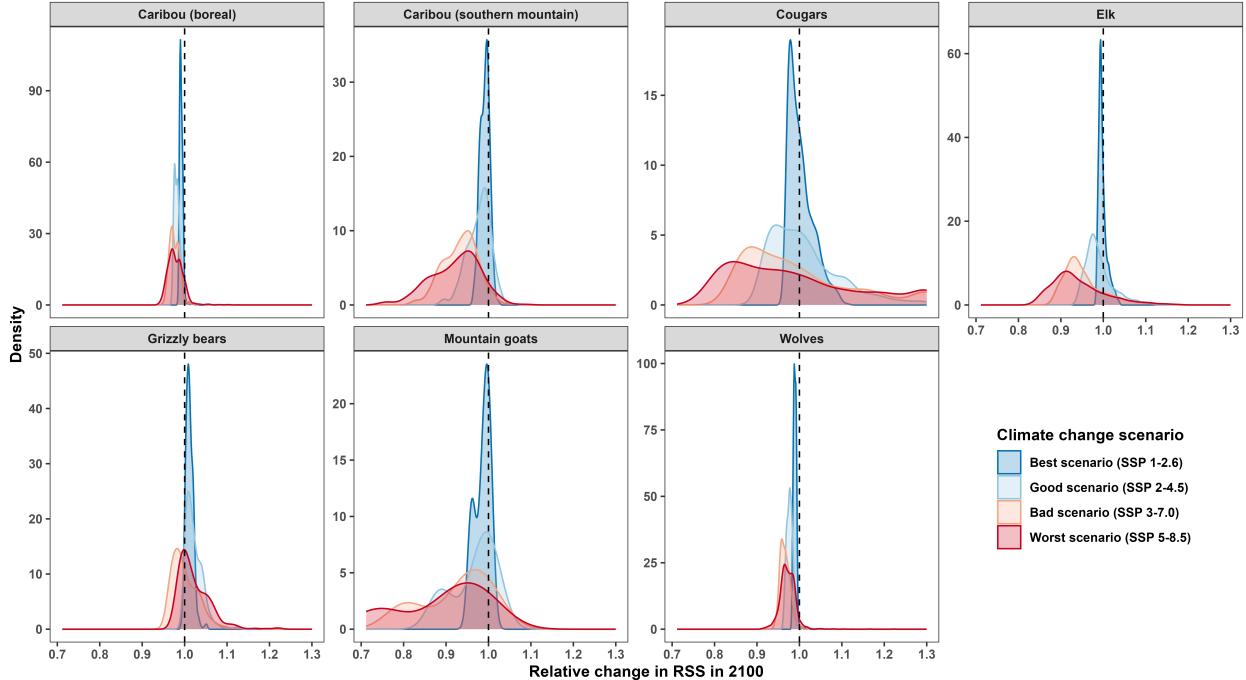


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each location’s 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).

385 responses of terrestrial mammals to temperature. In particular, tensor product interaction  
 386 terms were crucial for estimating smooth, nonlinear changes in daily and seasonal trends  
 387 with temperature. By allowing interaction terms to be smooth bivariate functions, we were  
 388 able to quantify changes in movement behaviour without the need to discretize time into  
 389 distinct windows (e.g., day/night and seasons). We were thus able to present changes using  
 390 relatively simple and interpretable surface plots (Figs. 3 and 4) that conveyed detailed and  
 391 nuanced estimates of change. This framework was essential for estimating how mammals  
 392 behave in extreme conditions for which data are scarce.

393 As temperatures warm, mammals’ risk of hyperthermia increases nonlinearly (Sherwood  
 394 & Huber, 2010), especially for large-bodied species (Alston *et al.*, 2020; Dyer *et al.*, 2023;  
 395 Verzuh *et al.*, 2023). The recent increase in frequency and duration of extreme-temperature  
 396 events (Bunnell *et al.*, 2011; Kienzle, 2018; Yao *et al.*, 2022; IPCC, 2023; Zhang *et al.*, 2023)  
 397 have forced many mammals towards increasingly atypical behaviours with long-term conse-

398 quences, ranging from changes in the behaviour and fitness of individuals (Cunningham *et*  
399 *al.*, 2021; Brivio *et al.*, 2024) to mass die-offs (Ameca y Juárez *et al.*, 2012). A species' abil-  
400 ity to respond to changing temperature and phenology depends mainly on its exposure,  
401 sensitivity, and adaptability to changes, and growing evidence suggests that many mammals  
402 in western Canada will struggle to respond due to limitations in all three factors (Ameca y  
403 Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Firstly, exposure to warming temperatures  
404 is widespread throughout the area, and warming is expected to accelerate over the coming  
405 decades (Bunnell *et al.*, 2011; Diffenbaugh & Field, 2013; Kienzle, 2018; Eum *et al.*, 2023;  
406 IPCC, 2023). Secondly, large-bodied mammals are particularly sensitive to high heat (Dyer  
407 *et al.*, 2023), but small-bodied mammals are also affected (Krebs *et al.*, 2019; Ratnayake  
408 *et al.*, 2019). Finally, species' adaptability is tested by the speed of climate change (Diff-  
409 enbaugh & Field, 2013) and the rigidity of many species' photoperiod-dependent phenology  
410 (Walker *et al.*, 2019).

411 Our results suggest that climate change will cause mammals to alter their seasonal move-  
412 ment behaviour, but not all species will respond similarly. For example, hotter temperatures  
413 caused boreal caribou to travel longer distances in fall, winter, and spring but less in sum-  
414 mer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.* (2021), and Lessard *et*  
415 *al.* (2025). The increase in movement rates during the colder seasons are likely partly due  
416 to shallower snow depth that results in greater mobility (Pedersen *et al.*, 2021), but rising  
417 temperatures during snowy seasons also increase the chances of rain-on-snow events, which  
418 limit forage availability and increase the ungulates' need to search for food (Stien *et al.*,  
419 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). In contrast, the reduced movement rates  
420 during warmer summers are likely mainly due to caribou searching for shelter from the heat  
421 due to ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023).  
422 The effects of extreme temperatures are exacerbated by phenological mismatches with sea-  
423 sonal photoperiod (Walker *et al.*, 2019), including the timing of molting and reproduction.  
424 Earlier growth seasons in boreal and arctic regions have resulted in lower calf birth and sur-

vival (Post & Forchhammer, 2008), while the lengthening of the growth season has allowed moose (*Alces alces*) and deer (*Odocoileus* spp.) to encroach on boreal caribou habitat, along with increased density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018; DeMars *et al.*, 2023). Thus, rising temperatures affect more than each individual species' movement behaviour; they have complex and interconnected effects on an entire community and its trophic structure.

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

Considerations about changes in trophic interactions leads to an important caveat about the results we present. The estimated effects of temperature on movement behaviour cannot be fully attributed to physiological responses to changes in temperature alone, since other aspects of habitats' seasonal phenology are (nonlinearly) correlated with temperature. For example, mountain goats' reduced movement rates at temperatures near 0°C in winter may be due to increased movement difficulty, since melting snow and rain-on-snow events affect

452 the energetic costs of movement (White, 2025) and encounter rates with predators (Sullender  
453 *et al.*, 2023). However, milder temperatures can also increase plant growth, which, in turn,  
454 allows goats to spend less time searching for forage (White *et al.*, 2025). Therefore, the  
455 figure 3 illustrates an estimate of the total effect of temperature on each species movement  
456 rates, but it does not explicitly account for energetic costs. Similarly, species' changes in  
457 habitat selection do not explicitly account for any changes in physiological or energetic costs.  
458 Both mountain goats and elk selected for higher elevation as temperatures warmed, but our  
459 models did not explicitly account for differences in forage availability at different altitudes.

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

478 Changes in mammals' seasonal movement behaviour are also likely to affect the timing

479 and frequency of human-wildlife interactions. Since heat affects mammals' sleep quality and  
480 likelihood to enter torpor (Fjelldal *et al.*, 2021; Wells *et al.*, 2022; Mortlock *et al.*, 2024),  
481 future decades may see increased levels of incidents with bears that struggle to enter or  
482 remain in hibernation (Johnson *et al.*, 2018). The risk is further increased when bears' are  
483 unable to meet their increased energetic requirements through foraging or hunting. Projected  
484 increases in park attendance due to rising temperatures and human population density in  
485 Western Canada are expected to further increase frequency of human-wildlife interactions  
486 (Weststrate *et al.*, 2024).

#### 487 4.1 Consequences for conservation

488 Species' adaptability to rising temperatures is challenged by the aforementioned simulta-  
489 neous, multifarious, and interconnected stressors caused by climate change, since responding  
490 to many concurrent changes at once is particularly difficult (Diffenbaugh & Field, 2013;  
491 Polazzo *et al.*, 2024). Locations may thus not be able to support species and population  
492 sizes they supported historically, and species may thus not select for historical geographical  
493 ranges in the future. It is therefore crucial for conservationists and other decision-makers to  
494 distinguish between a species' ideal environmental space (or E space, *sensu* Matthiopoulos,  
495 2022), and its best available geographic space (or G space, *sensu* Matthiopoulos, 2022). Ac-  
496 celerating multifarious change in species' movement behaviour and energetic costs require  
497 conservation measures to be proactive and anticipate future changes, even when future con-  
498 ditions are substantially different from historical conditions and historical data may not be  
499 available. To this end, the framework presented by Polazzo *et al.* (2024) for estimating  
500 species' responses to multifarious change becomes essential, particularly when accounting  
501 for energetic and fitness costs, as argued by Cunningham *et al.* (2021).

502 As of December 2024, only 13.8% of terrestrial Canada was within protected areas or  
503 other conserved areas (Environment and Climate Change Canada, 2025), so rapid action  
504 is necessary to protect additional 16.2% of Canada's land by 2030 in accordance with

505 Kunming-Montreal Global Biodiversity Framework (i.e., the “30 by 30 initiative”; Convention  
506 on Biological Diversity, 2022). However, the choice of what habitats to protect will re-  
507 quire careful consideration, since protected areas should support species not only in present  
508 conditions but also as species’ needs and selection change over the coming decades (Simmons  
509 *et al.*, 2021). As anthropogenic activity increasingly alters habitats and community struc-  
510 tures (Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022), protecting  
511 biodiversity and the habitats it depends on will require widespread and collaboration with  
512 local stakeholders, especially Indigenous Peoples, to ensure that all decisions are culturally  
513 sound and respect Treaties (Turner & Clifton, 2009; Desjardins *et al.*, 2020; Wong *et al.*,  
514 2020; Hessami *et al.*, 2021; Falardeau *et al.*, 2022; Lamb *et al.*, 2023). Understanding the  
515 consequences of climate change in mammalian movement behaviour is a first step towards  
516 proactively responding to how mammals will respond to human-induced rapid environmen-  
517 tal change (Sih *et al.*, 2011; Williams & Blois, 2018). However, a better understanding of  
518 such consequences will require a more holistic approach that includes careful data collection,  
519 model design, and interpretation and application of results.

## 520 4.2 Study strengths and limitations

521 Our results demonstrate that mammals respond to changes in temperature by altering  
522 how and where they move in complex and nonlinear ways (Figs. 3 and 4). Hierarchical Gen-  
523 eralized Additive Models were crucial in producing such results. The hierarchical approach  
524 us to produce statistically sound population-level estimates by accounting for differences in  
525 behaviour and data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020;  
526 Mortlock *et al.*, 2024; Jeltsch *et al.*, 2025; Silva *et al.*, 2025), while the flexibility of GAMs  
527 estimated mammals’ changes in movement behaviour without imposing rigid assumptions  
528 about the shape of the responses (Simpson, 2018, 2025). Still, GAMs’ flexibility and com-  
529 plexity can be a frustrating limitation if used too generously by inexperienced analysts. We  
530 suggest choosing the basis size ( $k$ ) for each smooth term carefully. While penalized splines

531 and REML can help avoid unruly smooth terms that would result in questionable estimates  
532 the penalty terms can struggle to restrict model complexity when datasets are particularly  
533 large (Wood, 2017; Wood *et al.*, 2017).

534 Despite the statistical soundness of the models, estimating mammals' response to pro-  
535 jected climate change remained a challenge because climate change projections included  
536 mean monthly temperatures but no measures of the full distribution of temperature. Since  
537 mammals' responses to temperature are nonlinear, accurate estimates of the effects of cli-  
538 mate change require estimates of the full distribution of temperatures that mammals will be  
539 exposed to – estimated means alone are not sufficient. This is because, since the responses  
540 to temperature are nonlinear, the mean response across the distribution of temperatures is  
541 not the same as the response to mean temperature. This inequality is often referred to as  
542 Jensen's inequality or the fallacy of the average (Jensen, 1906; Denny, 2019), and it is a  
543 main motivator for Generalized Linear Models and GAMs (Denny, 2017; Simpson, 2025).  
544 We approximated of the distribution of monthly temperatures by assuming monthly tem-  
545 peratures were normally distributed after estimating monthly variance in temperature, but  
546 more work is necessary on estimating changes in climate beyond montly mean values.

547 A second advantage of our approach is the use of continous-time estimates of speed  
548 and distance traveled that are less impacted by irregular sampling rates than straight-line  
549 displacement (Noonan *et al.*, 2019a). Still, our results indicate that the movement models fit  
550 by `ctmm` still suffer from two crucial issues. Firstly, although the models allow speeds to vary  
551 stochastically over time, they assume non-zero speeds and do not currently allow for multiple  
552 movement states (Auger-Méthé *et al.*, 2021). Secondly, while continuous-time estimates of  
553 speed are less sensitive to sampling rates than straight-line displacement estimates, our  
554 models indicate that longer sampling intervals still cause speed and travel distance to be  
555 underestimated (Fig. B8; also see DeNicola *et al.*, 2025). Shorter sampling intervals may  
556 help overcome this bias (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024). To account  
557 for the occasional missed GPS fix, we suggest setting sampling intervals to five or more

times smaller than the animal's expected directional persistence (Noonan *et al.*, 2019a). Still, excessively high sampling can cause the animal's movement to be confounded with GPS error (Fleming *et al.*, 2020), so we suggest calibrating GPS error whenever possible.

The final (and arguably most evident) limitation of our study was the use of temporally static estimates of forest cover. While the use of a single raster produced results and forecasts that are relatively simpler and easier to interpret, species' selection to estimated forest cover was relatively weak. Future studies should account for temporal variation in forest cover, especially given the growing severity of forest fires in Canada (Zurowski, 2023) as well widespread tree harvesting and its impact on wildlife (Betts *et al.*, 2022; Lochhead *et al.*, 2022). Additionally, a finer spatial scale may help detect changes in forest edge selection with greater precision. Future work would also benefit from accounting for other important forest properties, such as age, tree composition, and canopy height. However, accounting for more variables requires careful consideration about what values such variables should take when estimating changes in movement behaviour under future conditions.

### 4.3 Considerations for future work

#### **HERE**

We have presented a multi-species analysis of the effects of temperature on mammalian movement rates and habitat selection in hopes that other researchers can leverage this framework and models to expand our understanding of how temperature affects the movement behavior of other species, including smaller mammals, more elusive species, and non-mammal animals.

large mammals give clear responses, but they are also already studied most often

More work is necessary on quantifying interspecific responses to temperature, including the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of

584 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;  
585 Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at  
586 the current rate of climate change (Hatem *et al.*, 2014; Williams & Blois, 2018), especially  
587 since landscape changes will likely depend not only on the direct effect of temperature but  
588 also on cascading changes in the availability and unpredictability of resources (McLellan &  
589 McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

590 Future work should explore the effects of temperature on movement behaviour while  
591 accounting for finer-scale and species specific variables that were not accounted for in this  
592 study. Examples of these include temporally dynamic measures of forest type and age, canopy  
593 density, competitive pressures, forage availability, and predator avoidance, or environmental  
594 stochasticity. However, many of these data not available, so we also suggest that more  
595 work be done on quantifying such measures using spatiotemporally dynamic models and  
596 sufficiently fine resolutions. ... animals in the study are generalists; we need more work on  
597 specialists (i.e., species without wide species distributions) and smaller species, but they can  
598 be harder to track.

599 changes in the phenology of plants, fire, ice, or mammalian physiology (e.g., moulting,  
600 fat storage) or behaviour (e.g., migration, food caching), other than as direct responses to  
601 temperature.

## 602 Author contributions

603 SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote  
604 code for estimating instantaneous movement speeds. MJN conceived of the project idea and  
605 supervised SM throughout the project. All other authors contributed telemetry data and  
606 reviewed the interpretation of the results for their species of interest. KH and SD contributed  
607 substantially to manuscript review. All authors contributed to reviewing the manuscript.

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