

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; 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 (Deb  
46 *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations fail to  
47 adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable  
48 to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and responding  
49 to future changes require a comprehensive understanding of how temperature will affect how  
50 and where mammals move, as well as the implications such changes will have on species’  
51 adaptability and overall community structure. Recent work has documented the effects of  
52 climate change on mammals’ ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*,  
53 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size,

54 activity time, and elevational and latitudinal distribution McCain, 2019). However, there  
55 remains a need for fine-scale estimates of the effects of temperature on mammals' movement  
56 behaviour and quantitative predictions of how their behaviour will respond to climate change  
57 in the current century (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, understand-  
68 ing how temperature affects individual species is the first step towards understanding how  
69 temperature impacts the community dynamics (Hegel *et al.*, 2010; Carbeck *et al.*, 2022) and  
70 habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Merkle *et al.*, 2016; Slatyer *et*  
71 *al.*, 2022; Gerlich *et al.*, 2025), and how these changes will impact mammals in the coming  
72 decades (Sobie *et al.*, 2021; Eum *et al.*, 2023; Weststrate *et al.*, 2024).

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

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

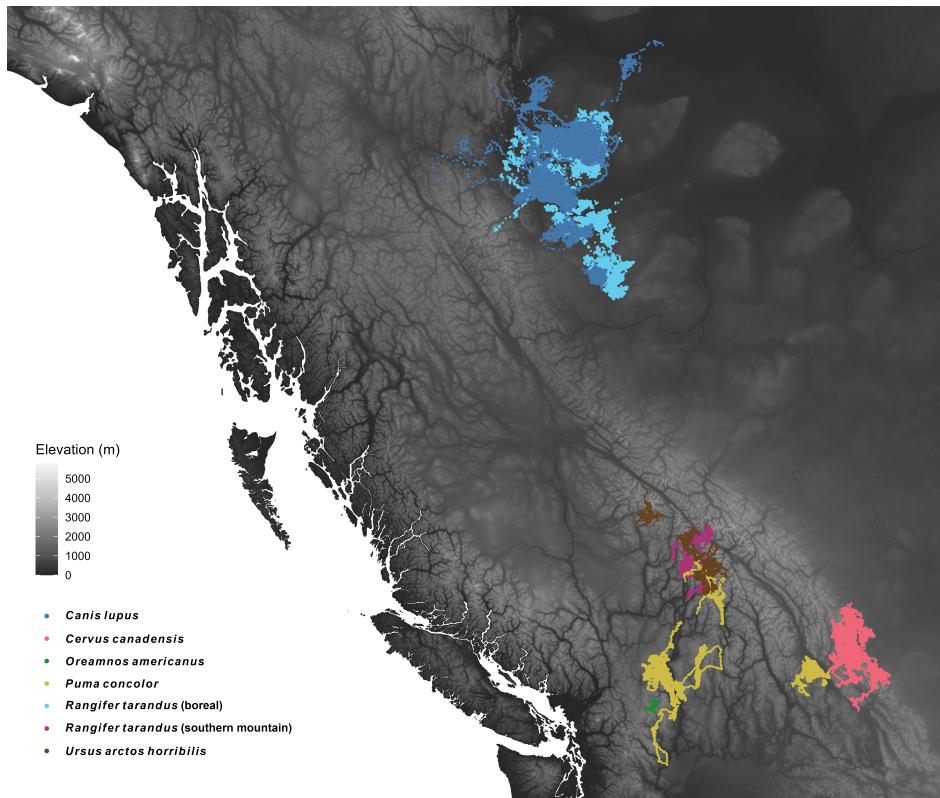


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	29	29

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

## 87 2 Methods

### 88 2.1 Datasets used

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

94 While we acknowledge there are other important variables (e.g., forest type, structure, and  
 95 age; terrain slope and aspect), we limited our models to only use three simple variables  
 96 for the sake of parsimony and comparability across species. See the discussion section for  
 97 additional detail on the advantages and limitations of using such simple models.

#### 98 2.1.1 GPS telemetry data

99 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
 100 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022). Boreal caribou (*Rangifer*  
*tarandus*) and wolf (*Canis lupus*) telemtries were acquired from a data repository of the  
 102 British Columbia Oil and Gas Research and Innovation Society (BC OGRIS) that was col-  
 103 lected as part of the boreal caribou radio-collaring program of the BC OGRIS Research  
 104 and Effectiveness Monitoring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON**  
 105 **OTHER TELEMETRY DATA.** From the full set of telemetry data, we removed a total  
 106 of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspect-

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

### 112 2.1.2 Historical temperature data and climate change projections

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

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

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

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

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

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

152 **2.1.3 Resource rasters**

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

166 **2.2 Estimating mammals' instantaneous speeds**

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

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

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

183 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

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

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

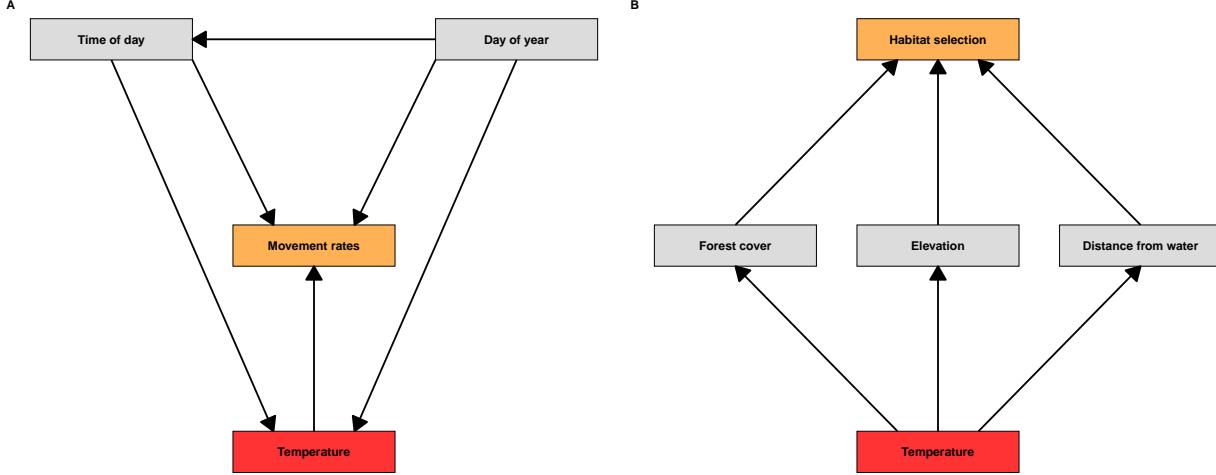


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

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

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

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

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

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

238 **2.3.2 Effects of temperature on habitat selection**

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

251 Each species' model had the same structure:

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

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

### 264 3 Results

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

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

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

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

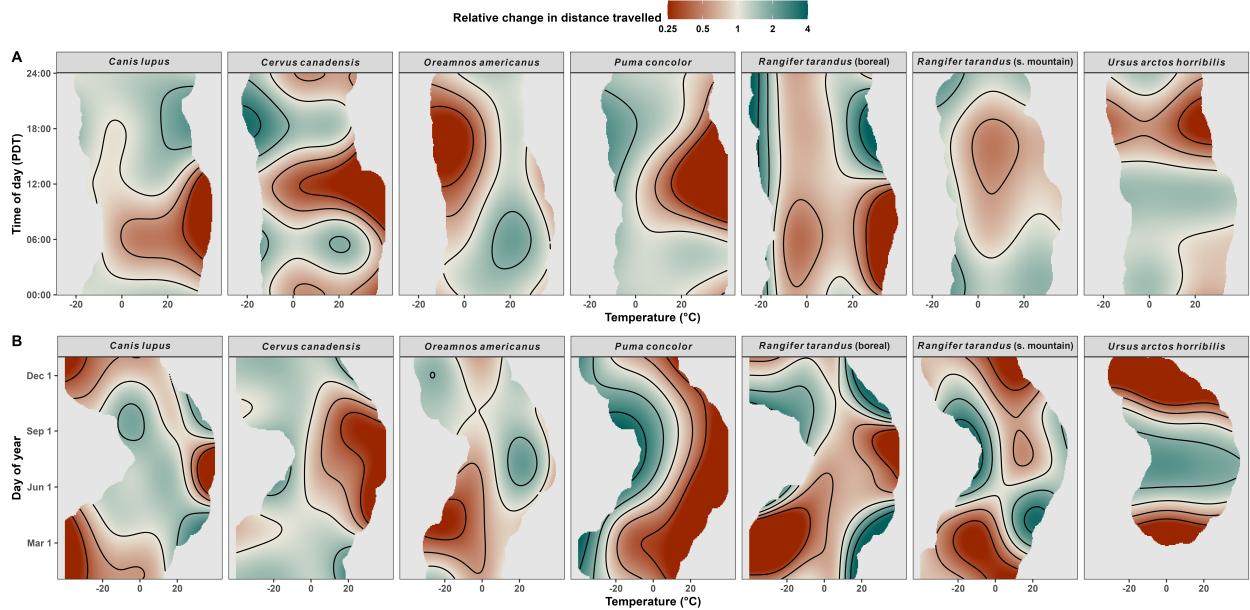
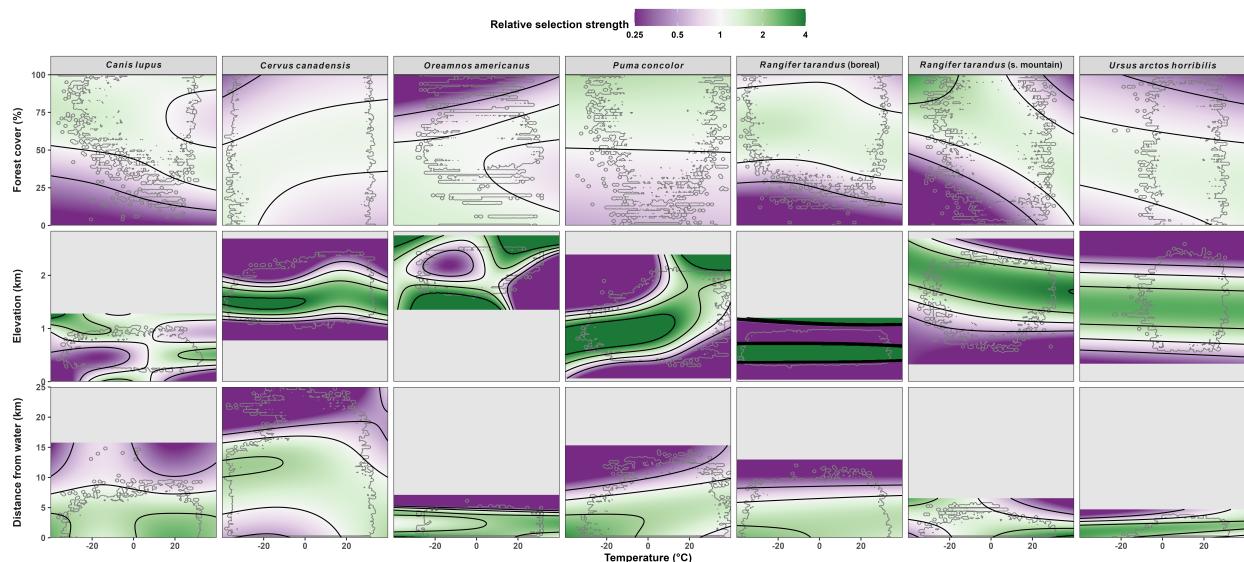


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year at 12:00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

### 312 3.2 Effects of temperature on habitat selection

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

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

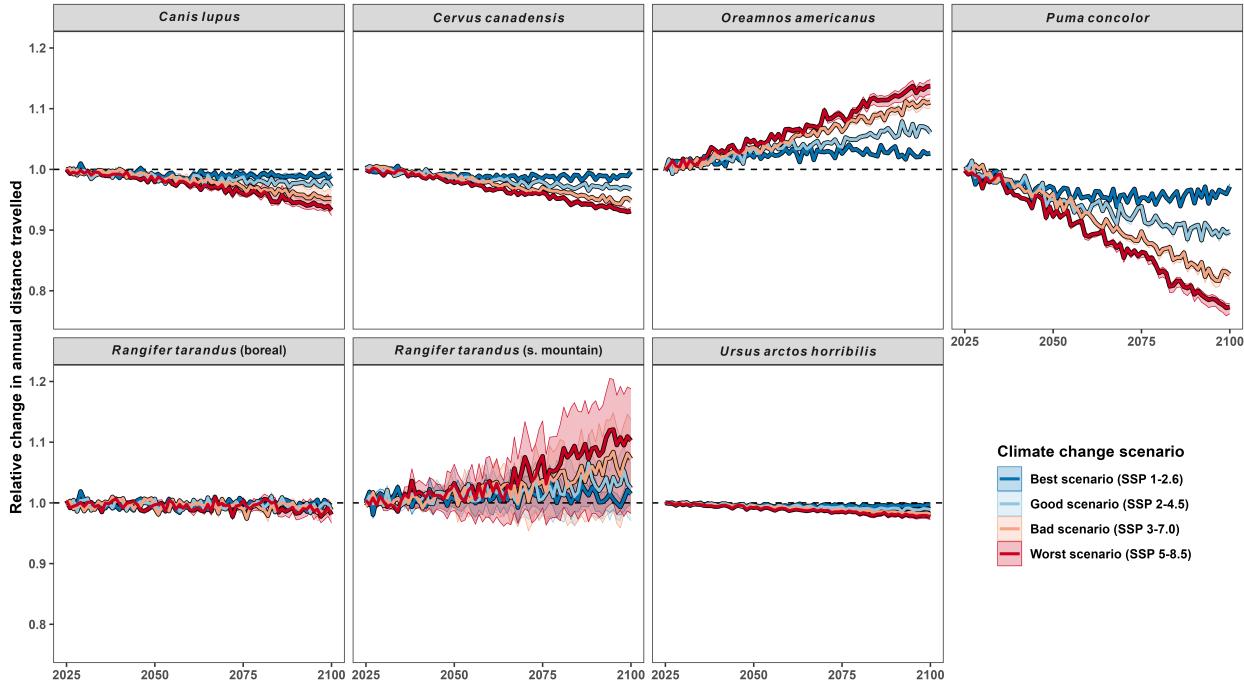


Figure 5: Species will adapt their movement rates differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the median change in distance travelled (probability of moving times speed when moving) due to predicted changes in temperature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

344 Median RSS was projected to decrease over time within the each species' observed range,  
 345 but, again, changes were stronger under worse SSPs (Fig. 7). Decreases were most pro-  
 346 nounced in areas with the lowest RSS and most severe for elk, mountain goats, pumas, and  
 347 southern mountain caribou. Changes for boreal wolves and caribou were relatively negli-  
 348 gible. Elk, cougars, and grizzly bears were predicted to increase their selection strength  
 349 for top-RSS areas, and elk, mountain goats, cougars, and southern mountain caribou were  
 350 predicted to further decrease their selection for areas with low RSS. Unsurprisingly, the  
 351 change in RSS between 2025 and 2100 also varied spatially for all species (Fig. 8). Overall,

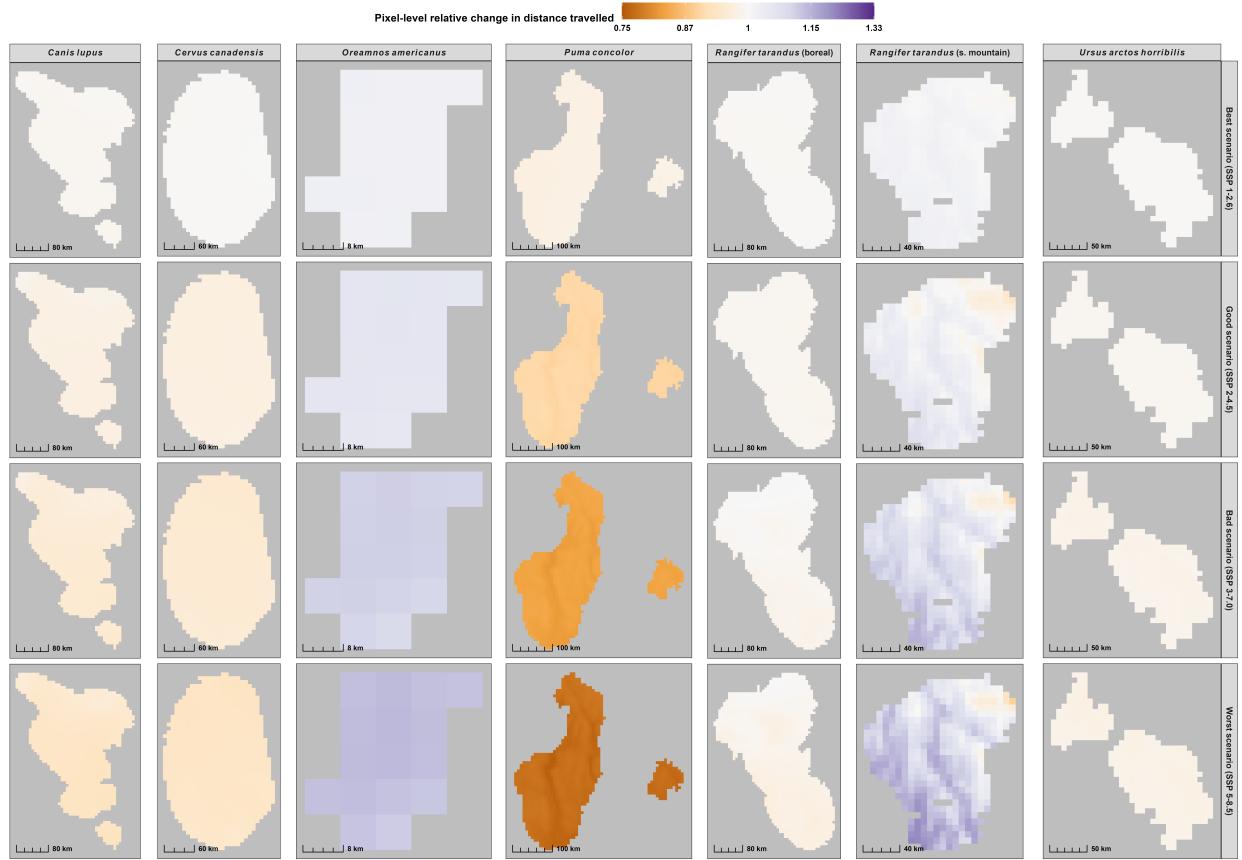


Figure 6: **Climate change will impact each species' movement rates differently, but changes will also vary spatially.** The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values  $< 1$  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).

352 RSS decreased throughout most of each species' current range, although elk, cougars, and  
 353 bears were predicted to increase their selection for higher-altitude habitats. Still, none of  
 354 the species were projected to increase RSS throughout their habitat (9).

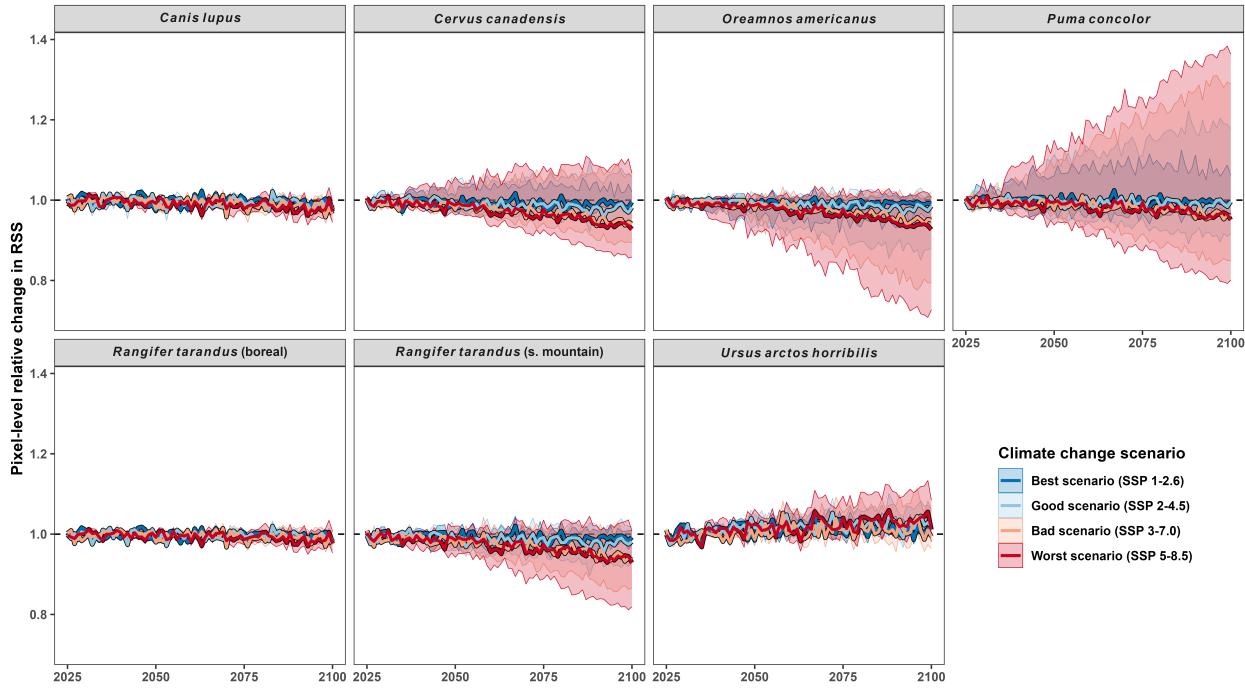
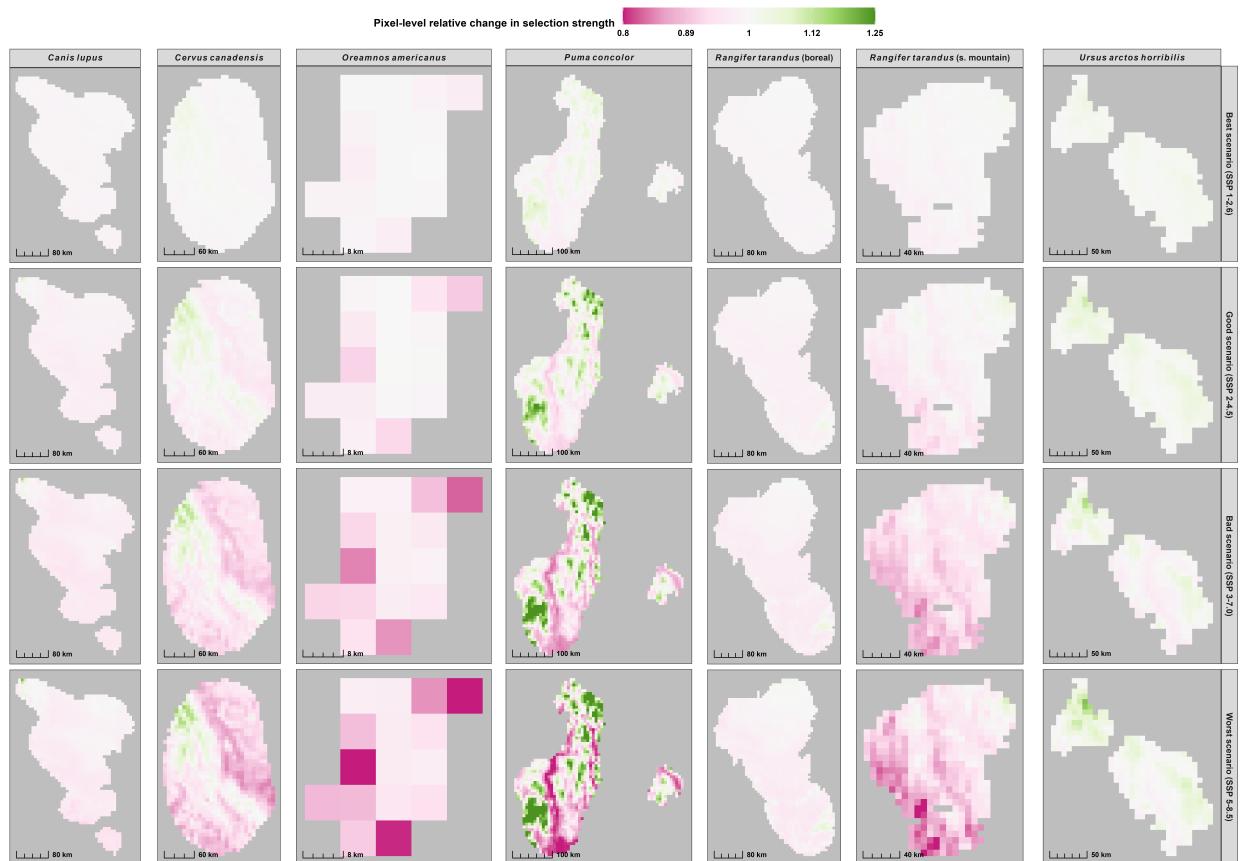


Figure 7: Species will adapt their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas 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).

## 355 4 Discussion

356 We have demonstrated that temperature is an important determinant of how and where large  
 357 mammals move, including how they alter seasonal and daily cycles in movement behavior.  
 358 However, predicting mammals' responses to climate change becomes increasingly complex  
 359 as habitats warm and animals are increasingly frequently exposed to extreme and novel  
 360 conditions.

361 ***Temperature affects many aspects of mammalian physiology and behaviour,  
 362 including energetics, sleep, and movement behaviour. Climatic changes during  
 363 the last two centuries have exposed many mammals to novel and increasingly***



**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).

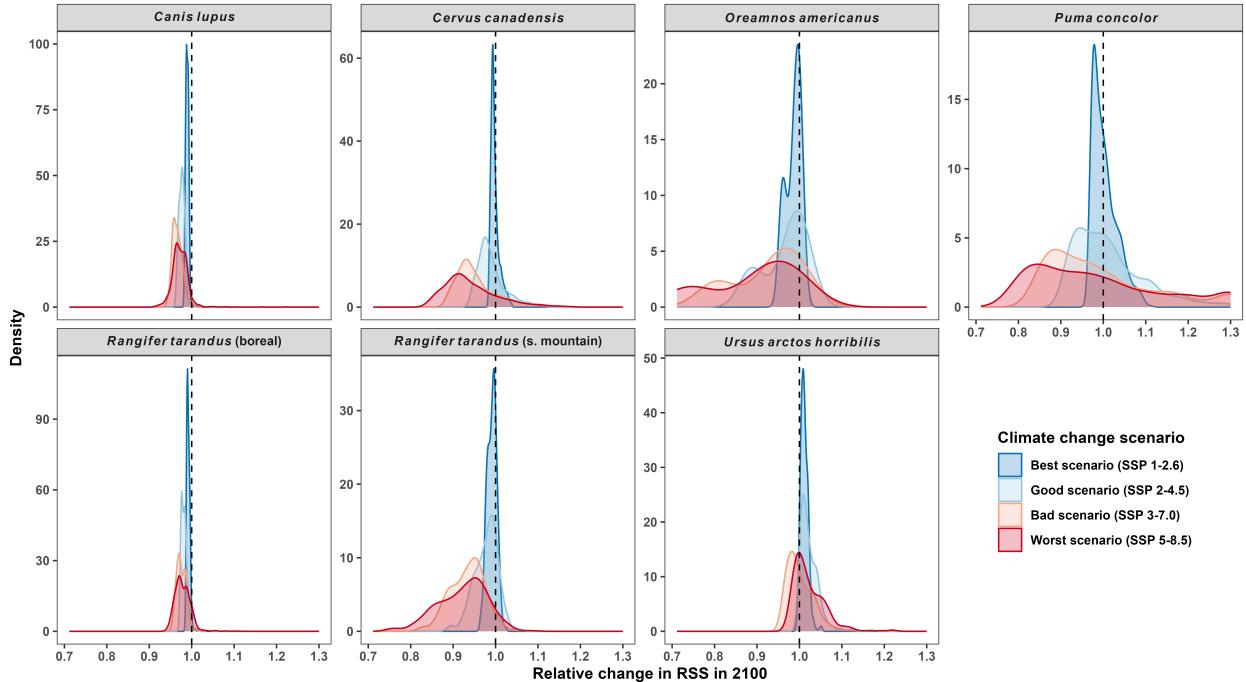


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species' change in RSS in 2100 for their current habitat (Fig. 8), relative to each location's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

364 *extreme environmental conditions that have led to visible changes that impact*  
 365 *not only individuals but also ecological and human communities. However,*  
 366 *quantifying the effects of climate change is often complex, especially as con-*  
 367 *ditions become increasingly different and extreme events become increasingly*  
 368 *common. Accurately quantifying the nonlinear effects of temperature on how*  
 369 *and where mammals move requires careful data collection and model design.*  
 370 *We have presented a multi-species analysis of the effects of temperature on*  
 371 *mammalian movement rates and habitat selection. Understanding of how*  
 372 *temperature affects each species in a community will allow us to begin making*  
 373 *community-level inferences of how temperature will affect intra-specific inter-*  
 374 *actions from a movement behaviour perspective (Nathan et al., 2008, 2022;*  
 375 *Martinez-Garcia et al., 2020). While adopting such a perspective is surely not*  
 376 *simple, it would result in more complete estimates of the effects of climate*  
 377 *change on community ecology, particularly when species are exposed to rapid*

378 *change in many important variables. Future work should explore the effects*  
379 *of temperature on movement behaviour while accounting for finer-scale and*  
380 *species specific variables that were not accounted for in this study. Examples*  
381 *of these include temporally dynamic measures of forest type and age, canopy*  
382 *density, competitive pressures, forage availability, and predator avoidance, or*  
383 *environmental stochasticity. However, many of these data not available, so*  
384 *we also suggest that more work be done on quantifying such measures using*  
385 *spatiotemporally dynamic models and sufficiently fine resolutions.*

386 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3  
387 and 4 comes with substantial uncertainty, particularly given that the responses are nonlin-  
388 ear. At warm temperatures, mammals overheat (Alston *et al.*, 2020; Dyer *et al.*, 2023), so  
389 their movement behaviour and that of their competitors, predators, and/or prey can often  
390 be substantially different from the behaviour at typical temperatures. As extreme temper-  
391 ature events become more frequent and prolonged throughout the year (Yao *et al.*, 2022;  
392 IPCC, 2023), mammals will be increasingly forced towards atypical behaviours that may al-  
393 ter community structures and behaviours, both during such events and afterwards (Logares  
394 & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance, changes in climate  
395 and phenology impact the life history and behaviour of many hibernating mammals (Wells  
396 *et al.*, 2022), and hot weather can also affect mammals' sleep quality and likelihood to enter  
397 torpor (Fjelldal *et al.*, 2021; Mortlock *et al.*, 2024).

398 Changes in mammal movement behaviour may also alter the frequency and intensity  
399 of human-wildlife conflict, especially with the addition of growing pressures from human  
400 development and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024).  
401 At the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et*  
402 *al.*, 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease  
403 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being  
404 preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;

405 Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;  
406 Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences  
407 for population and ecosystem structures and dynamics as prey, predators, and competitors  
408 experience altered seasonal cycles and increasingly common climate “weirding” (Bunnell *et*  
409 *al.*, 2011).

410 *Protecting a third of the world’s ecosystems in accordance with the*  
411 *Kunming-Montreal Global Biodiversity Framework (Convention on Biological*  
412 *Diversity, 2022) appears less achievable as global political and environmental*  
413 *conditions change rapidly and unpredictably (Sih *et al.*, 2011; Simmons *et**

414 *al.*, 2021; Guenette *et al.*, 2022; Sovacool *et al.*, 2023). Achieving the “30  
415 *by 30” goal will require international collaboration (Huang & Zhai, 2021) as*  
416 *well as active partnership with local Peoples, especially Indigenous Peoples*  
417 *(Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences of*  
418 *climate change on mammals’ movement behaviour is a first step towards*  
419 *proactively responding to how mammals will respond to human-induced rapid*  
420 *environmental change (Sih *et al.*, 2011; Williams & Blois, 2018).*

#### 421 4.1 Effects of temperature on movement rates

422 The heterogeneity mammals’ responses to temperature suggests that ecological communities  
423 will respond to change in complex and interconnected ways. Although our models do not  
424 account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that  
425 warmer temperatures cause many species to alter their daily and seasonal activity patterns  
426 (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C,  
427 cougars moved most at night, but when temperatures were below 0°C they tended to move  
428 more throughout the day. Throughout the year, they adapted their tolerance to temperature  
429 and moved less when it was relatively hot (for a given time of year), especially in spring and  
430 summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and

boreal caribou when summer temperatures were above 20°C suggests that the increasingly common and intense heat waves across western Canada will have community-wide impacts on movement rates, encounter rates, and potentially community structure (Martinez-Garcia *et al.*, 2020). 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 hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially since landscape changes will likely depend not only on the direct effect of temperature but also on cascading changes in the availability and unpredictability of resources (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

#### 444 4.2 Effects of temperature on habitat selection

445 *Overall, estimated selection strength was weakest for forest cover and*  
446 *strongest for elevation. Elevation is the only raster that doesn't change no-*  
447 *ticeably over time, so time-varying rasters of the other two would have likely*  
448 *given stronger (and better) estimates.*

449 As with the effects of temperature on movement rates, the heterogeneity of temperature  
450 effects on species' habitat selection indicates that efficient and proactive habitat conservation  
451 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
452 physiological responses to temperature that may impact movement, such as changes in the  
453 phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or  
454 behaviour (e.g., migration, food caching), other than as direct responses to temperature.  
455 Consequently, the behavioural changes we present should be interpreted carefully. While  
456 some seasonal cycles do not depend directly on temperature and may thus not be impacted

457 directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the  
458 predictions we present also rely on the assumption that mammals will not adapt these  
459 seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage  
460 availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important  
461 to stress the distinction between habitat selection and quality. While individuals tend to  
462 select for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength  
463 can also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,  
464 2021).

- 465 • geographic space *sensu* Matthiopoulos (2022)  
466 • environmental space *sensu* Matthiopoulos (2022)  
467 • G space is the realization of the theoretical E space

#### 468 4.3 Predicted changes in movement during the 21<sup>st</sup> century

469 Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on  
470 Biological Diversity, 2022) will require careful planning but often also rapid action. As  
471 of December 2024, only 13.8% of terrestrial Canada was within protected areas or other  
472 conserved areas (Environment and Climate Change Canada, 2025). Additionally, efficient  
473 and effective conservation will require collaboration with Indigenous and local communities  
474 to ensure Treaties are respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020;  
475 Falardeau *et al.*, 2022; Lamb *et al.*, 2023) and as we actively prepare for future change  
476 (Desjardins *et al.*, 2020; Hessami *et al.*, 2021).

477 ... spatial and intra-individual variation should be accounted for when deciding the lo-  
478 cation and size of protected areas (Jeltsch *et al.*, 2025). Population-level means that ignore  
479 such variation can greatly limit the efficacy of conservation projects (Muff *et al.*, 2020; Mort-  
480 lock *et al.*, 2024; Silva *et al.*, 2025). Additionally, accurate estimates of the effects of changes  
481 in temperature on mammals’ movement require a holistic view of the direct effects of tem-  
482 perature on mammals’ movement directly as well as its effects on other drivers of movement,

such as forage and prey availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*, 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*, 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation among the responses of different species (and individuals), especially as populations undergo a rapid cascade of change (Botero *et al.*, 2015) and mammals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and likely decreases), some individuals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased risk of extirpation or extinction (Duncan *et al.*, 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

#### 4.4 Species-specific considerations

- Cougars: attraction for disconnected patches of high elevation could lead to fragmentation or traps
- boreal caribou: Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000 m, but such a selection is only possible if: (1) such habitats exist in the individuals' range, and (2) crossing the 500 m to > 1,000 m regions is safe and attractive
- sm caribou: HRSFs do not account for migratory behaviour due to reproduction or predation risk

#### 4.5 Study limitation and considerations for future studies

Our work highlights three central considerations for future research: (1) telemetry sampling rates should be designed primarily in relation to the movement timescales of the species

of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of individuals tracked and the duration of each telemetry should depend not just on population size but also the 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

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

## 541 5 Other refs

- 542 • Eum *et al.* (2023) “Potential changes in climate indices in Alberta under projected  
543 global warming of 1.5–5 °C”
- 544 • climate change threatens biodiversity of marine mammals: [https://doi.org/10.1038/  
545 s41598-019-57280-3](https://doi.org/10.1038/s41598-019-57280-3)
- 546 • marine turtles shift and lose habitat with temperature: [https://www.science.org/doi/  
547 10.1126/sciadv.adw4495](https://www.science.org/doi/10.1126/sciadv.adw4495)
- 548 • Walker *et al.* (2019): Global climate change and invariable photoperiods: {A} mis-  
549 match that jeopardizes animal fitness

## 550 6 Author contributions

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

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