

# Rising temperatures alter how and where boreal 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 and community dynamics. Previous studies have estimated the effects of temperature on mammalian movement behaviour, but few disentangled them from seasonal behaviour cycles. Consequently, it is still uncertain how mammals will adapt their movement behaviour throughout the 21<sup>st</sup> century. We address this gap by quantifying the effects of temperature on the movement rates and habitat selection of six large-bodied mammalian species (boreal and southern mountain caribou, cougars, elk, grizzly bears, mountain goats, and wolves) throughout western Canada between 1998 and 2023. We show that temperature significantly affected how and where these boreal mammals moved, and we predict that climate change will impact mammals' movement behaviour throughout the 21<sup>st</sup> century. Projected responses to climate change suggested that rising temperatures will drive southern mountain caribou and mountain goats to move more, while cougars, elk, and wolves will move less. Boreal caribou and grizzly bears showed little change in projected yearly movement rates but clear shifts in phenology. We also predict that rising temperatures will reduce median habitat selection strength for four of the species, although cougars and elk are expected to show increased selection strength for higher altitudes. As mammals increasingly alter their movement rates and select against portions of their current ranges, changes in individuals' movement behaviour will impact encounter rates, including predator-prey dynamics and human-wildlife interactions. Conservation efforts should therefore account for future changes in movement behaviour as well as the consequences such changes may have on communities. Anticipating changes in mammalian movement behaviour will become crucial for effectively and proactively understanding community-level responses and selecting high-quality habitat for long-term conservation.

## <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> (Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-Herrera *et al.*, 2020; Pe-  
<sup>6</sup> terson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). How and where animals move  
<sup>7</sup> thus also determines encounter rates with resources (Mezzini *et al.*, 2025), humans (Johnson  
<sup>8</sup> *et al.*, 2018; Weststrate *et al.*, 2024), predators, prey, and competitors (Martinez-Garcia *et*  
<sup>9</sup> *al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). However, ambient temperature affects  
<sup>10</sup> animals' movement rates by altering the energetic cost of movement and thermoregulation  
<sup>11</sup> (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher,  
<sup>12</sup> 2022), and extreme temperatures can impact animals' movement rates (Dyer *et al.*, 2023),  
<sup>13</sup> phenology (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Johnson *et al.*, 2018; Carbeck  
<sup>14</sup> *et al.*, 2022), and life history (Newediuk *et al.*, 2024), and even cause physiological damage  
<sup>15</sup> and death (Hetem *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*,  
<sup>16</sup> 2020; Schwerdt *et al.*, 2024). Animals may search for a short-term buffer from extreme  
<sup>17</sup> temperatures by moving to thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias  
<sup>18</sup> *et al.*, 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), and shelter may even be  
<sup>19</sup> preferred over forage abundance (Hall *et al.*, 2016). However, climate change during the last  
<sup>20</sup> century (IPCC, 2023) has caused animals to alter how and where they move as they respond  
<sup>21</sup> to hotter temperatures and increasingly severe and frequent extreme-heat events (Bunnell  
<sup>22</sup> *et al.*, 2011; Thompson *et al.*, 2022; IPCC, 2023).

<sup>23</sup> Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood  
<sup>24</sup> & Huber, 2010). While extreme cold often leads to reduced movement, provided that in-  
<sup>25</sup> dividuals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou  
<sup>26</sup> *et al.*, 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological

27 damage in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et*  
28 *al.*, 2021; Newediuk *et al.*, 2024). Mammals' homeothermy can cause them to have difficulty  
29 dissipating heat, particularly when ambient temperatures are near or above body tempera-  
30 ture. Larger-bodied mammals are more likely to alter their movement behaviour with rising  
31 temperatures, since they tend to move long distances (Merkle *et al.*, 2016), are particularly  
32 sensitive to overheating (Fuller *et al.*, 2016; Alston *et al.*, 2020; Verzuh *et al.*, 2023), and  
33 their movement rates are thus strongly limited by excessive heat (Dyer *et al.*, 2023).

34 Global warming during the last century has resulted in milder and shorter winters, hotter  
35 and longer summers, and a greater risk of extreme-heat events (IPCC, 2023), with widespread  
36 changes in mammals' phenologies, circadian rhythms, fitness, and life histories (Botero *et al.*,  
37 2015; McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Wells *et al.*, 2022; Newediuk *et al.*,  
38 2024). However, behavioural responses to heat vary substantially across species depending  
39 on body size, vagility, and activity times (McCain & King, 2014; Williams & Blois, 2018).  
40 For example, warming temperatures have allowed deer (*Odocoileus* spp.) to shift northward,  
41 which has led to increased density of wolves (*Canis lupus*) and higher predation on caribou  
42 (*Rangifer tarandus caribou*) (Latham *et al.*, 2011; Barber *et al.*, 2018; Dickie *et al.*, 2024).  
43 Preparing for and responding to future changes will require a detailed understanding of  
44 not only how and where mammals move throughout the thermal landscape but also  
45 the cascade of effects that such changes will have at the population and community levels  
46 (Cunningham *et al.*, 2021).

47 As heat stress intensifies throughout the 21<sup>st</sup> century, mammals will continue to suffer  
48 impacts on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-  
49 Durand *et al.*, 2020). It remains unclear how or whether species will be able to respond to  
50 climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh  
51 *et al.*, 2023), especially if populations fail to adapt (Botero *et al.*, 2015; Sawyer *et al.*, 2019)  
52 or are physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015;  
53 Williams & Blois, 2018). Recent work has documented the effects of climate change on

54 mammals' ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and  
55 movement behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there  
56 remains a need for fine-scale estimates of the effects of temperature on mammals' movement  
57 behaviour and quantitative predictions of future changes in movement behaviour.

58 In this paper, we quantify the effects of proximal air temperature on mammalian move-  
59 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial  
60 mammal species in western Canada (boreal and southern mountain caribou, cougars: *Puma*  
61 *concolor*, elk: *Cervus canadensis*, grizzly bears: *Ursus arctos horribilis*, mountain goats:  
62 *Oreamnos americanus*, and wolves; Table 1). Western Canada is currently experiencing  
63 accelerating and widespread but spatially heterogeneous warming (Turner & Clifton, 2009;  
64 Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (plants: Post & Forchhammer,  
65 2008; Tysor, 2025; ice: Basu *et al.*, 2024), and more frequent and intense extreme heat  
66 events (Zhang *et al.*, 2023). Decision makers must understand which areas will best sustain  
67 and protect biodiversity not only for current conditions but future decades, too. Failing to  
68 understand how climate change will affect mammalian movement behaviour will hinder our  
69 ability to respond to the current climate crisis and make decisions that are viable in the  
70 long term. Furthermore, understanding how temperature affects individual species is the  
71 first step towards understanding how temperature impacts the community dynamics (Hegel  
72 *et al.*, 2010; Cunningham *et al.*, 2021; Carbeck *et al.*, 2022) and phenology (Bunnell *et al.*,  
73 2011; Duncan *et al.*, 2012; Merkle *et al.*, 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and  
74 how these changes will impact mammals in the coming decades (Sobie *et al.*, 2021; Eum *et*  
75 *al.*, 2023; Weststrate *et al.*, 2024).

Table 1: Summary statistics of each species' set of GPS data, namely: the start and end of each set of GPS telemetry data, the number of GPS fixes (after data cleaning), 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	Fixes	$\Delta t$ (hours)	Animals	Has speed
Caribou (boreal)	2011-03-02	2018-01-03	200,561	13.00	146	131

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

## 76 2 Methods

### 77 2.1 Datasets used

78 In this study, we estimate how temperature affected mammals' probability of moving,  
 79 speed when moving, and habitat selection by leveraging three datasets: (1) a multi-species  
 80 collection of 25 years of GPS telemetry data throughout a large spatial range of western  
 81 Canada (Fig. 1), (2) historical, hourly air temperature data from the ERA5 reanalyzed  
 82 dataset (Hersbach *et al.*, 2023), and (3) temporally static rasters of percent forest cover,  
 83 elevation, and distance from water. We then forecast each species' movement behaviour  
 84 throughout the 21<sup>st</sup> century using monthly climate change projections under four Shared  
 85 Socioeconomic Pathways (SSPs; Riahi *et al.*, 2017; Mahony *et al.*, 2022): SSP 1-2.6 ("Sus-  
 86 tainability – Taking the Green Road"; low challenges to mitigation and adaptation), SSP  
 87 2-4.5 ("Middle of the Road: medium challenges to mitigation and adaptation"), SSP 3-7.0  
 88 ("Regional Rivalry – A Rocky Road"; high challenges to mitigation and adaptation), and  
 89 SSP 5-8.5 ("Fossil-fueled Development – Taking the Highway"; high challenges to mitigation,  
 90 low challenges to adaptation).

91 We acknowledge that our models of habitat selection ignore many important variables of  
 92 habitat selection (e.g., forest type, structure, and age; terrain slope and aspect; prey avail-  
 93 ability; population density). We limited our models to only use three simple and temporally  
 94 static rasters to produce simple and easily interpretable estimates and forecasts under the  
 95 assumption of temporally invariant landscapes.

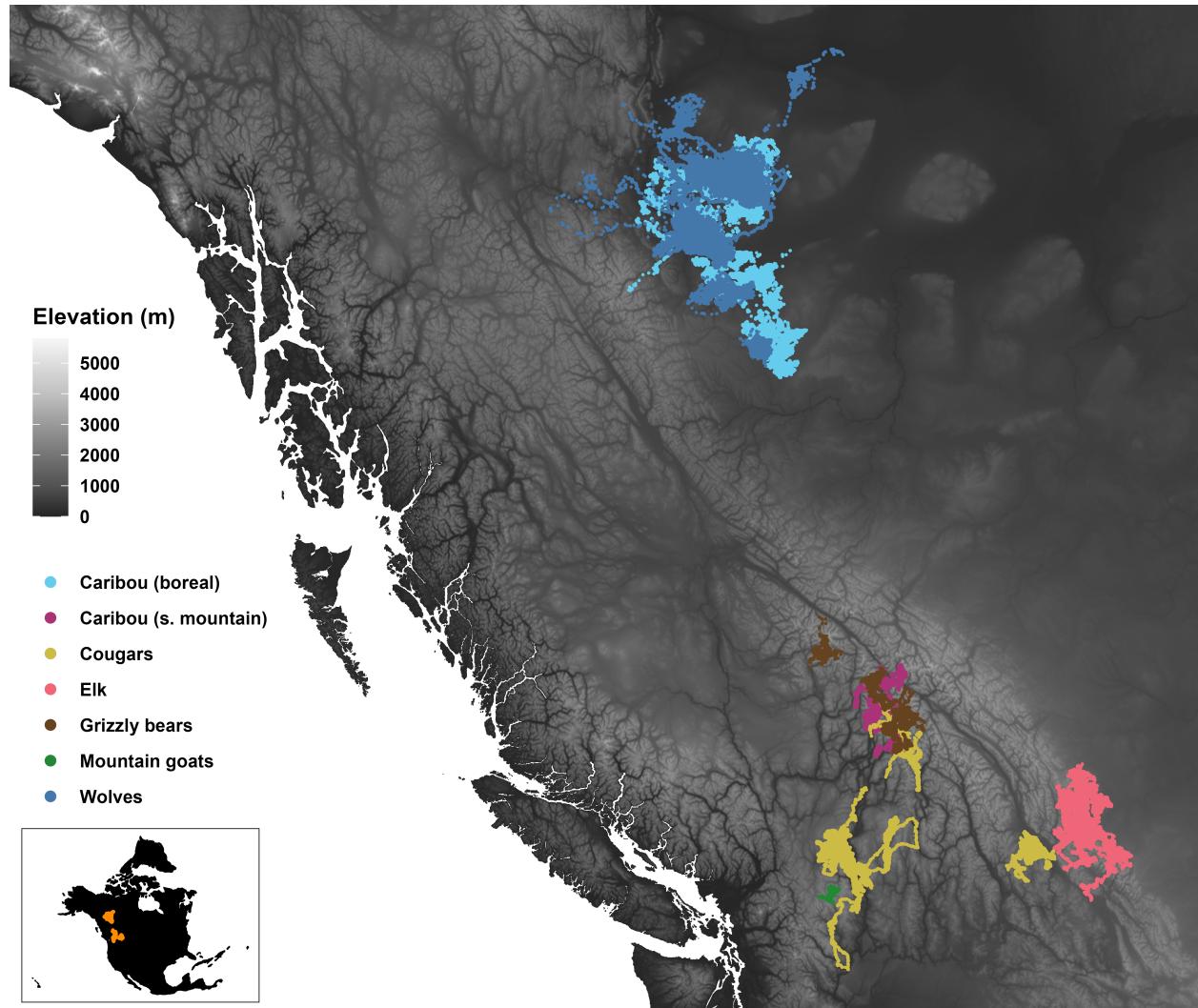


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area. The inset in the bottom left shows the telemetry data within the north american continent. Both maps use the BC Albers Equal Area Conic projection (EPSG:3005).

96 **2.1.1 GPS telemetry data**

97 Boreal caribou and wolf telemetry data were acquired from a data repository of the British  
98 Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected as  
99 part of the boreal caribou radio-collaring program of the BC OGRIS Research and Effec-  
100 tiveness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data  
101 were obtained from Ford *et al.* (2023). Cougar data are from Darlington *et al.* (2025) and  
102 (**serrouya\_ref?**). Elk data from the work of Ciuti *et al.* (2012) were downloaded from  
103 Movebank (Kays *et al.*, 2022). Finally, grizzly bear telemetry data are from (**ref?**), while  
104 mountain goat data are from (**ref?**).

105 From the full set of telemetry data, we removed 2,396 problematic GPS locations (0.16%,  
106 including collar calibration data) after inspecting diagnostic plots of (1) distance from the  
107 median location, (2) straight-line displacement between locations, (3) turning angle, and  
108 (4) time interval between consecutive points. Particular attention was paid to points with  
109 large turning angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially if  
110 antecedent and subsequent points indicated relatively stationary behaviour (Appendix A).

111 **2.1.2 Historical temperature data and climate change projections**

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

118 To obtain projected average monthly temperatures from 2025 to 2100 at a  $0.08^\circ$  spatial  
119 resolution, we used the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and ClimateNA  
120 v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only  
121 included estimates of future monthly averages, a scale substantially coarser than that of our

tracking data (Table 1). To estimate the distribution of temperatures at an hourly scale within a month, we assumed values to be approximately normally distributed with mean  $\mu_T$  and variance  $\sigma_T^2$ . We estimated  $\mu_T$  using the ClimateNA projections, while we estimated  $\sigma_T^2$  by modeling the observed variance in historical weather data for western Canada from 1998 to 2023 (inclusive). For each location  $\langle x, y \rangle$  and month  $m$  of each year (e.g., the observed variance at coordinates  $\langle -119.40, 49.94 \rangle$  in April 2005), we calculated the variance in historical temperature data, for a total of  $(2024 - 1998) \times 12 = 312$  observations per location. We then modeled  $\sigma_T^2$  a Generalized Additive Model (GAM) for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017) fitted with 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 complete model for the distribution of projected temperature was thus

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

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

149 We simulated hourly variation in future years by assuming hourly temperature followed  
150 a normal distribution with mean specified by the monthly **climatenetR** climate projections  
151 and variance as specified by the gamma GAMLS. For each month within each year from  
152 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the  
153 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the  
154 normalized Gaussian probability density for each quantile.

### 155 2.1.3 Habitat rasters

156 We estimated percent forest cover and distance from water using the temporally static  
157 rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing  
158 the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-  
159 ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted  
160 the raster of percent cover of open water (class 12) to a binary raster of pixels with water  
161 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance from  
162 the nearest pixel with water using the **distance()** function from the **terra** package. Fi-  
163 nally, we obtained two digital elevation models using the **get\_elev\_raster()** function from  
164 the **elevatr** package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6  
165 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of 0.08°)

166 for downloading climate change projections via `climatenetR`. All final rasters and code are  
167 available on GitHub (see the Data Availability Statement). For ease of interpretability and  
168 comparison with current conditions, we assumed resources would remain constant through  
169 to 2100, although we recognize that the spatial distribution of forest cover and open water  
170 will change throughout the 21<sup>st</sup> century.

171 **2.2 Estimating mammals' instantaneous speeds**

172 We modeled each animal's movement using continuous-time movement models (Fleming  
173 *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for R. We then  
174 estimated each mammal's instantaneous speed at each observed location by applying the  
175 `ctmm::speeds()` function on all models with finite speed estimates (415 of 433; Fleming *et*  
176 *al.*, 2014; Noonan *et al.*, 2019a). The remaining 18 movement models had sampling rates that  
177 were too coarse, relative to the animals' directional persistence, to reconstruct the animals'  
178 movement trajectories (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; DeNicola *et al.*, 2025).  
179 The models were for one mountain goat, 15 boreal caribou, and two southern mountain  
180 caribou (Table 1).

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

190 **2.3 Estimating the effects of temperature on mammals' movement behaviour**

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

202 To assess the importance of including temperature as an explicit covariate (as opposed  
203 to including its effects with time of day and day of year), we fit models with and without  
204 smooth effects of temperature and compared the fits of the two sets of models via analyses  
205 of deviance (a form of generalized likelihood ratio tests) following the methods of Section  
206 3.3 in Wood (2017). See Appendix B for additional information.

207 **2.3.1 Effects of temperature on movement rates**

208 We estimated the effects of temperature on mammals' instantaneous movement state (mov-  
209 ing or not) and speed when moving using two Hierarchical Generalized Additive Models  
210 (HGAMs; Pedersen *et al.*, 2019 and Appendix B) with the `mgcv` package for R. The first  
211 HGAM estimated the probability that an animal was moving,  $P(M)$ , with a binomial fam-  
212 ily of distributions and logit link function. The second HGAM estimated an animal's speed  
213 when moving with a gamma family of distributions and log link function. We fit the models  
214 with fast Restricted Maximum Likelihood ('fREML') and discretized covariates (`discrete =`  
215 `TRUE`) to optimize computational efficiency with no appreciable losses to model performance

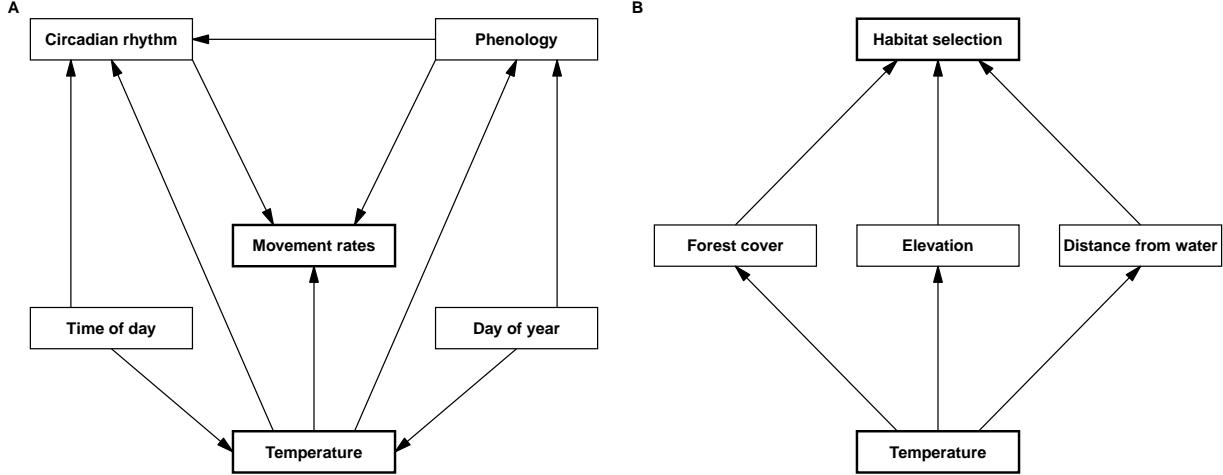


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (red) on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and their product: hourly distance traveled). The effects of temperature on mammals' movement rates depend on circadian rhythm and phenology, since animals may respond to temperatures differently at different times of day and or days of year. Additionally, both temperature and phenology depend on time of day and day of year. Finally, circadian rhythm changes with seasonal phenology due to changes in photoperiod (e.g., the time of twilight changes throughout the year, affecting crepuscular activity). (B) Similarly, habitat selection depends on the availability and selection of habitat variables (forest cover, elevation, and distance from water), but the selection strength for each variable is conditional on temperature. For example, an animal may select for more densely-forested areas at extreme temperatures. The resource selection functions for (B) also included marginal smooths of temperature to account for sampling biases across seasons.

216 (Appendix B; Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM  
 217 and the gamma HGAM inform us on an animal's long-term average speed, since it is the  
 218 product of the probability of moving and its average speed when moving.

219 The HGAMs (equations (2) and (3)) included fixed-effect intercepts for each species  
 220 ( $\beta_s$ ), random intercepts for each animal ( $Z_a$ ), and species-level **by** smooths that allowed  
 221 independent smoothness parameters for each species (model I in Figure 4 of Pedersen *et*  
 222 *al.*, 2019). The **by** smooths accounted for trends in time of day (in Pacific Daylight Time;  
 223 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time  
 224 of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017).  
 225 The models also had three tensor product interaction terms by each species: (1) day of year  
 226 and time of day, (2) temperature and time of day, and (3) temperature and day of year.  
 227 These three terms accounted for smooth changes in: (1) daily behaviour across day of year,  
 228 (2) the response to temperature over time of day (e.g., changes in nocturnality), and (3)

229 the response to temperature over day of year (e.g., the timing of molting, migration, and  
 230 hibernation). Finally, two smooth terms of log-transformed sampling interval ( $\text{dt}$ ; hours)  
 231 corrected for biases in speed estimates arising from irregular GPS sampling intervals, since  
 232 longer intervals result in lower speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025).  
 233 A global smooth term of  $\log(\text{dt})$  accounted for the overall effect of sampling interval, while  
 234 a factor-smooth interaction term ( $\text{bs} = \text{'fs'}$ ) of  $\log(\text{dt})$  and species accounted for species-  
 235 level deviations from the global term while assuming a common smoothness parameter across  
 236 species (model GS in Figure 4 of Pedersen *et al.*, 2019). Formally, the model for movement  
 237 state  $M$ , with  $M = 0$  indicating no movement and  $M = 1$  indicating movement, was

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

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

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

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

243 **2.3.2 Effects of temperature on habitat selection**

244 We estimated the effects of temperature on each species' selection for percent forest  
245 cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water  
246 (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for  
247 each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family  
248 of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing  
249 non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation  
250 in the telemetry locations by weighting each point based on the telemetry's Autocorrelated  
251 Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,  
252 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature  
253 points were used to approximate the likelihood function of a Poisson point process through  
254 Monte-Carlo Markov chain-based integration (Aarts *et al.*, 2008; Fithian & Hastie, 2013;  
255 Baddeley *et al.*, 2015) and were determined using the raster cells in each animal's 99.9%  
256 AKDE percentile, with each raster cell having a weight of 1. The number of quadrature  
257 locations greatly outnumbered the number of observed locations (Fig. B12), especially after  
258 accounting for the AKDE weights (Fig. B13).

259 Each species' model had the same structure:

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

where  $O$  indicates whether an animal was observed ( $O = 1$ ) or not ( $O = 0$ ), and the species-level indices are omitted for readability, but each term in the model can be assumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`), elevation (`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). All species' estimated probability of moving and speed when moving decreased with sampling intervals above 1 hour, except for cougars' speed, although the estimated trends were highly uncertain (Fig. B8). Consequently, we present all results while predicting specifically for one-hour sampling intervals. At 0°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 overall speed (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°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 hourly 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 of  $T = 0^{\circ}\text{C}$ .

Species	$n$	T < $-20^{\circ}\text{C}$ (%)	T > $+20^{\circ}\text{C}$ (%)	$\hat{P}(M = 1 T)$	$\hat{\mathbb{E}}(S M = 1, T)$	$\hat{\mathbb{E}}(D T)$
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			

Across all species, Relative Selection Strength (RSS) was weakest for forest cover and strongest for elevation. At temperatures near 0°C, boreal caribou selected for forest cover between 50% and 75%, elevations near 500 m, and distances from water  $< 10$  km, while southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances from water  $\lesssim 5$  km. Cougars selected for dense forest cover ( $> 75\%$ ), an elevation of  $\sim 1$

km, and distances from water < 7.5 km. Elk selected for intermediate forest cover ( $\approx$  50%), elevations between 1 and 2 km, and distances from water of 10-15 km. Grizzly bears selected for relatively sparse forest cover (25-50%), elevation between 1 and 2 km, and distances from water < 3 km. Mountain goats selected for sparse forest cover (< 25%), elevations near 1.5 km, and distances from water < 5 km. Finally, wolves selected for forest cover ( $\gtrapprox$  50%), elevations near 1 km, and distances from water < 5 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  $\Delta AIC \geq 342$ ; Appendix B). Accounting for temperature even resulted in a simpler HRSF for mountain goats (lower model degrees of freedom due to simpler random smooth terms) 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]. All species altered their daily and seasonal movement behaviour to changes in temperature (Fig. 3). The response was most visible in cougars. In late spring (June 1<sup>st</sup>), they moved from evening to early morning if hourly 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. Overall, uncertainty around the estimated effects was generally higher at extreme temperatures due

320 to lower data availability (Figs. B4A, B5A, and B6A).

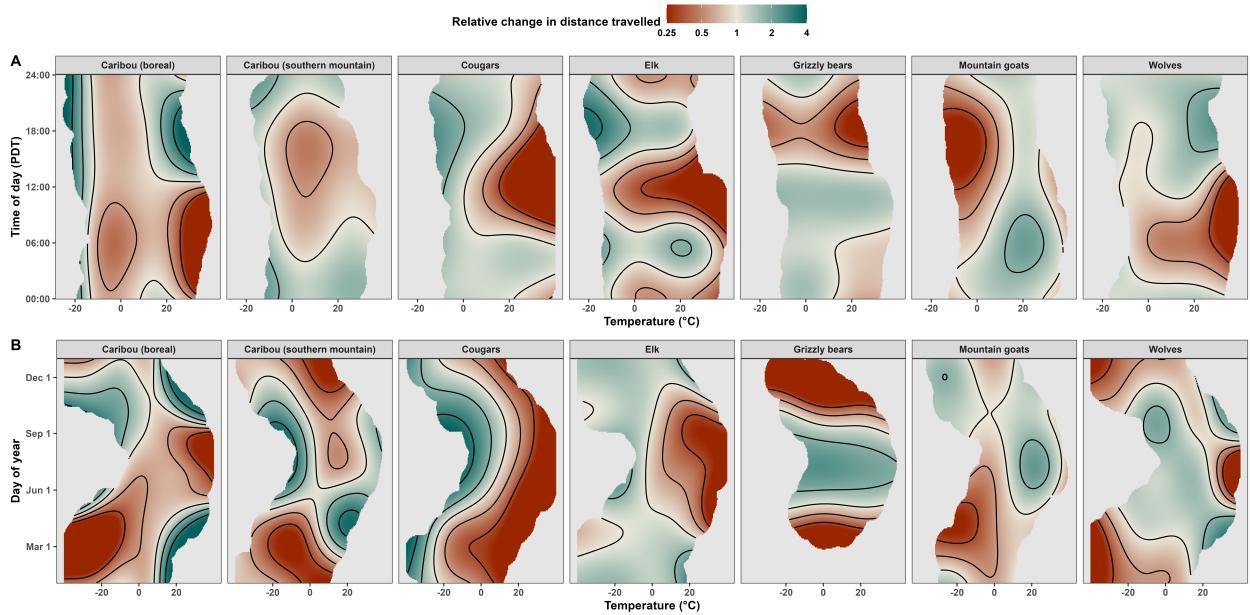
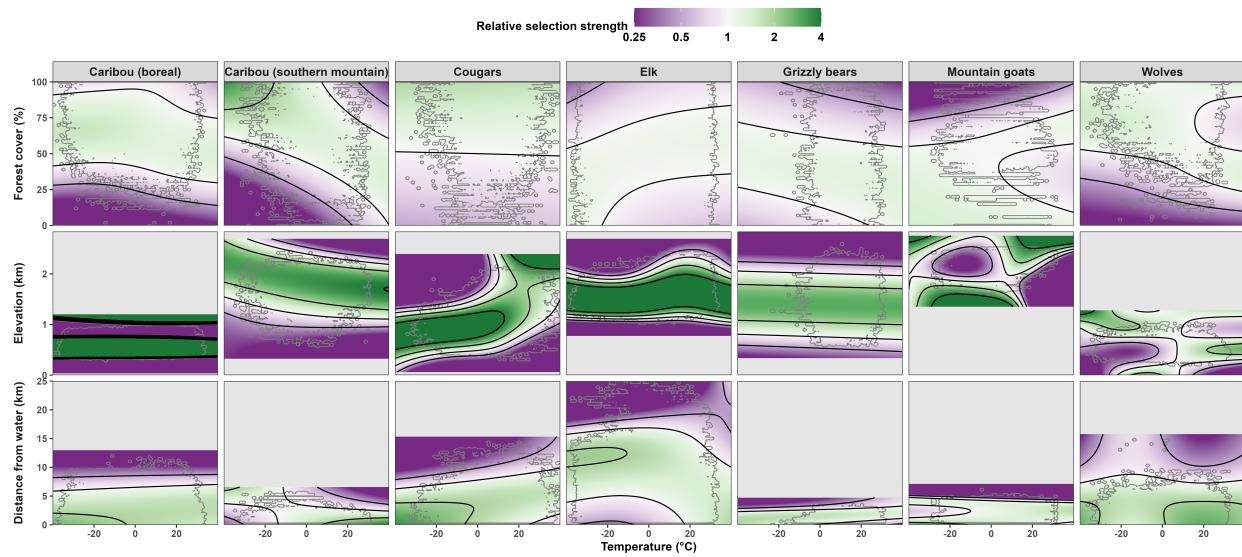


Figure 3: **Temperature is a strong driver of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in hourly distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year at 12:00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

### 321 3.2 Effects of temperature on habitat selection

Species' RSS was generally strongest for elevation and weakest for forest cover, but RSS depended significantly on temperature for all species (all p-values <  $2.2 \times 10^{-16}$ ; Fig. 4). Changes in RSS with temperature were strongest for elevation and generally weakest for distance from water, but there were no common trends across all species for any of the three resources. All species except cougars exhibited clear temperature-dependent shifts in their preference for forest cover. At higher temperatures, wolves relaxed their preference for forested areas, while mountain goats relaxed their preference for 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 were scarcer (Fig. B15).

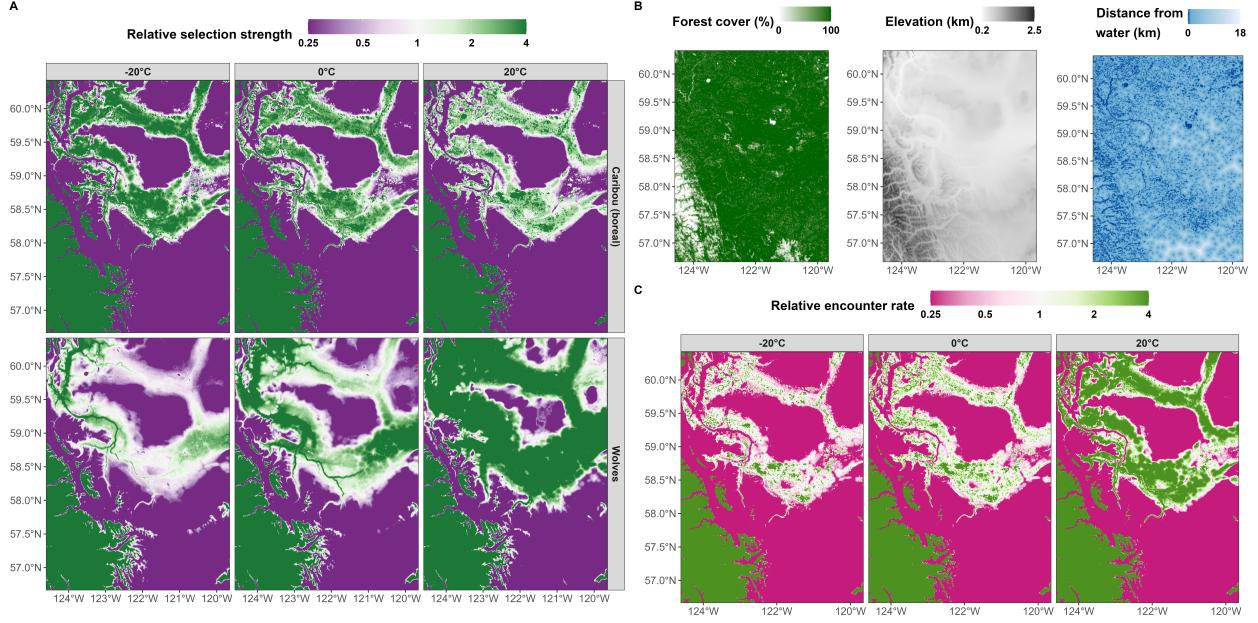


**Figure 4: Mammals' habitat selection depends on ambient temperature.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered and capped to between 0.25 and 4 ( $2^{\pm 2}$ ) to improve readability.

Fig. 5 presents the predicted habitat selection for boreal caribou and wolves. Overall, both species selected for the same low-elevation area (< 500 m; Fig. 5A-B), but caribou generally avoided the river system that wolves were often found at, and their selection strength varied with temperature. As wolves' habitat selection strengthened at warmer temperatures, encounters at 20°C were approximately four times more frequent than at -20°C, independent of changes in the species' movement rates (Fig. 5C).

### 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

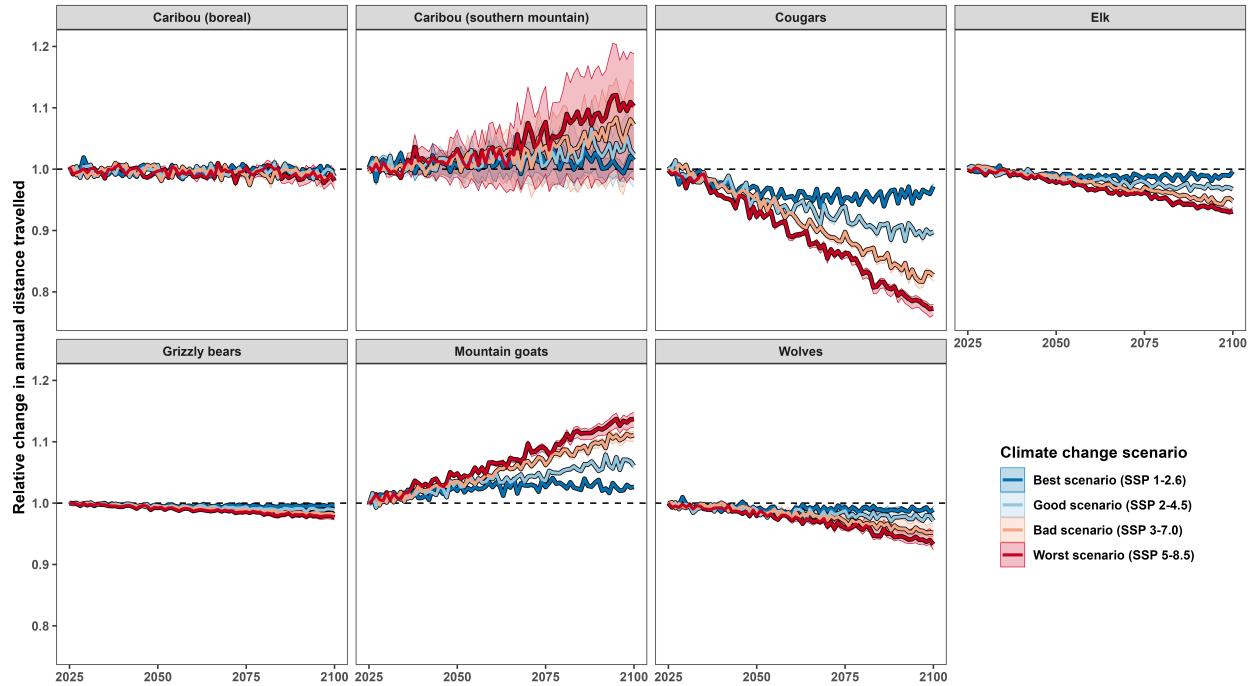


**Figure 5: Temperature affects boreal caribou's and wolves' habitat selection and, consequently, their encounter rates.** Panel (A) shows the rasters of the three habitat variables used in the hierarchical resource selection functions, while panel (B) shows the relative selection strength (RSS) for boreal caribou and wolves, as a function of temperature. RSS values were re-centered and capped to between 0.25 and 4 ( $2^{\pm 2}$ ) to improve readability. Finally, panel (C) shows the (scaled) product of the RSS values in panel (B) as a proxy for encounter rates between individuals of the two species.

(Fig. 6). 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 yearly distance traveled were negligible for boreal caribou and grizzly bears, although both species showed seasonal changes in seasonal movement rates. As temperatures warmed, boreal caribou were predicted to move more in winter, spring, and fall but less in summer (Fig. 3), while grizzly bears were predicted to show 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. 7). 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.

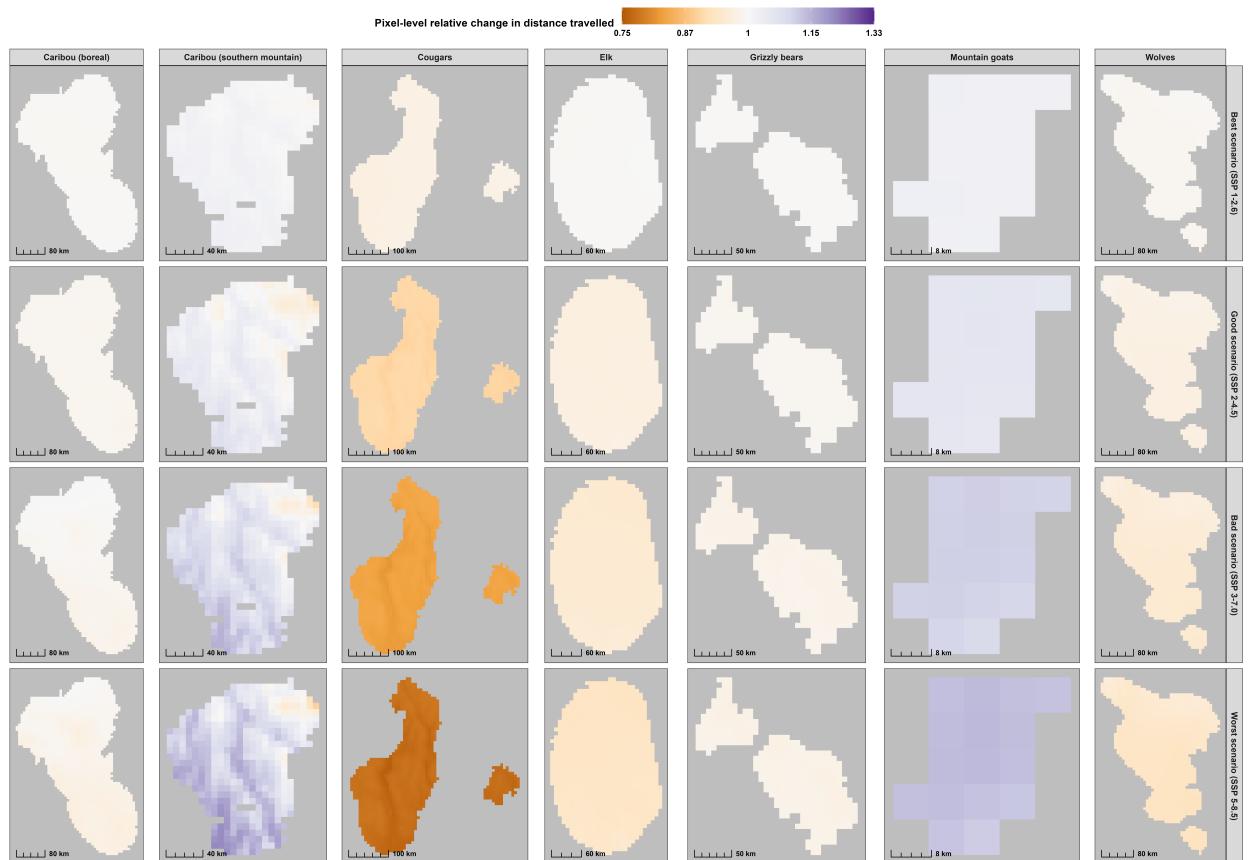
Absolute relative changes in predicted yearly distance travelled were small under the best-case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars).

362 Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change  
 363 projections (Fig. 7). Again, absolute changes were generally greatest under worse SSPs, but  
 364 the direction of change at each location also varied across SSPs (most visible in cougars).



**Figure 6: Species are predicted to alter their movement rates differently in response to climate change, and worse climate-change scenarios will result in the greatest change.** Bold lines indicate the median change in yearly distance travelled (probability of moving times speed when moving) due to predicted changes in temperature within each species' study area. 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.

365 Median RSS was projected to decrease over time within each species' observed range, but,  
 366 again, changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced  
 367 in areas with the lowest RSS and most severe for elk, mountain goats, cougars, and southern  
 368 mountain caribou. Changes for boreal wolves and caribou were negligible. Elk, cougars,  
 369 and grizzly bears were predicted to increase their selection strength for top-RSS areas, and  
 370 elk, mountain goats, cougars, and southern mountain caribou were predicted to further  
 371 decrease their selection for areas with low RSS. Unsurprisingly, the predicted change in  
 372 RSS between 2025 and 2100 also varied spatially for all species (Fig. 9). Overall, RSS  
 373 decreased throughout most of each species' current range, although elk, cougars, and bears



**Figure 7: Climate change is predicted to 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 cover. All maps extend to each species' study area (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

374 were predicted to increase their selection for higher-altitude habitats. Still, none of the  
 375 species were projected to increase RSS throughout their habitat (10).

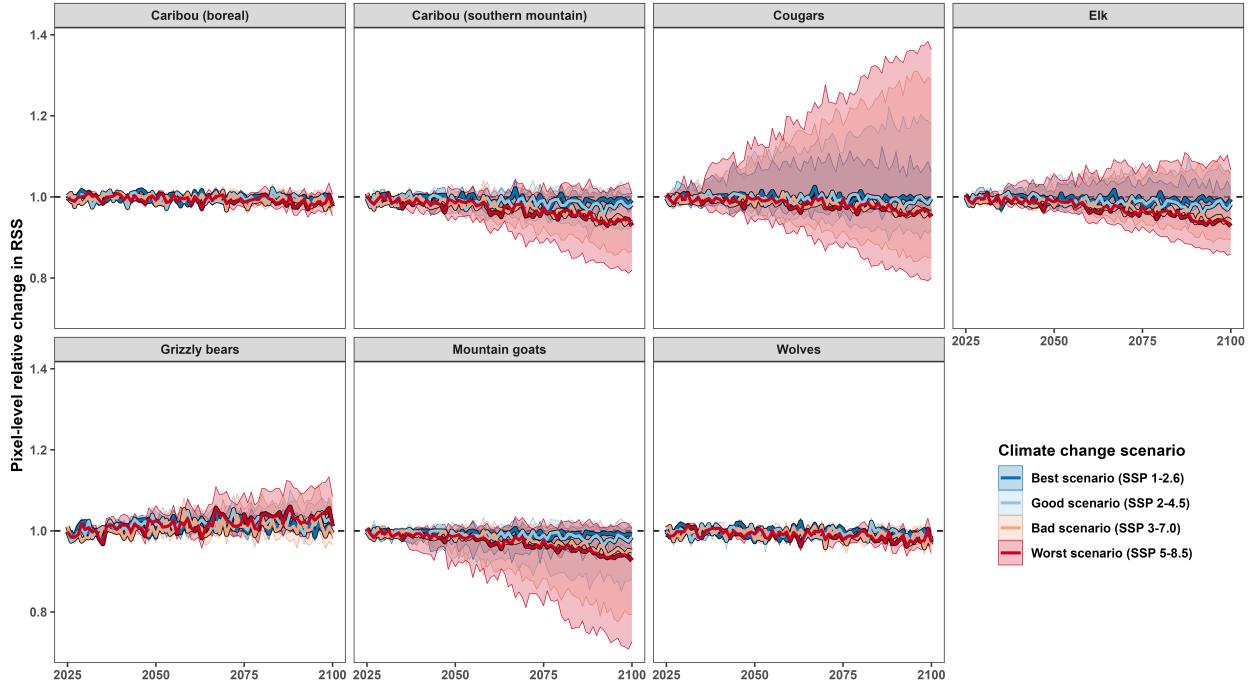


Figure 8: **Species are predicted to alter their habitat selection differently in response to climate change, and worse climate-change scenarios will result in the greatest change.** Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' study area. 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).

## 376 4 Discussion

377 We have demonstrated that temperature is an important driver of how and where large bo-  
 378 real mammals move, and that it affects mammals' seasonal and daily movement behaviour  
 379 in complex and nonlinear ways. However, predicting mammals' responses to climate change  
 380 remains a challenge, as habitats are warming rapidly and mammals are exposed to increas-  
 381 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,  
 382 2023). We leveraged the flexibility and interpretability of HGAMs to estimate mammals'  
 383 nonlinear responses to temperature without imposing rigid assumptions about the shape of  
 384 the responses (Simpson, 2018, 2025). In particular, tensor product interaction terms were



**Figure 9: 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' study area and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

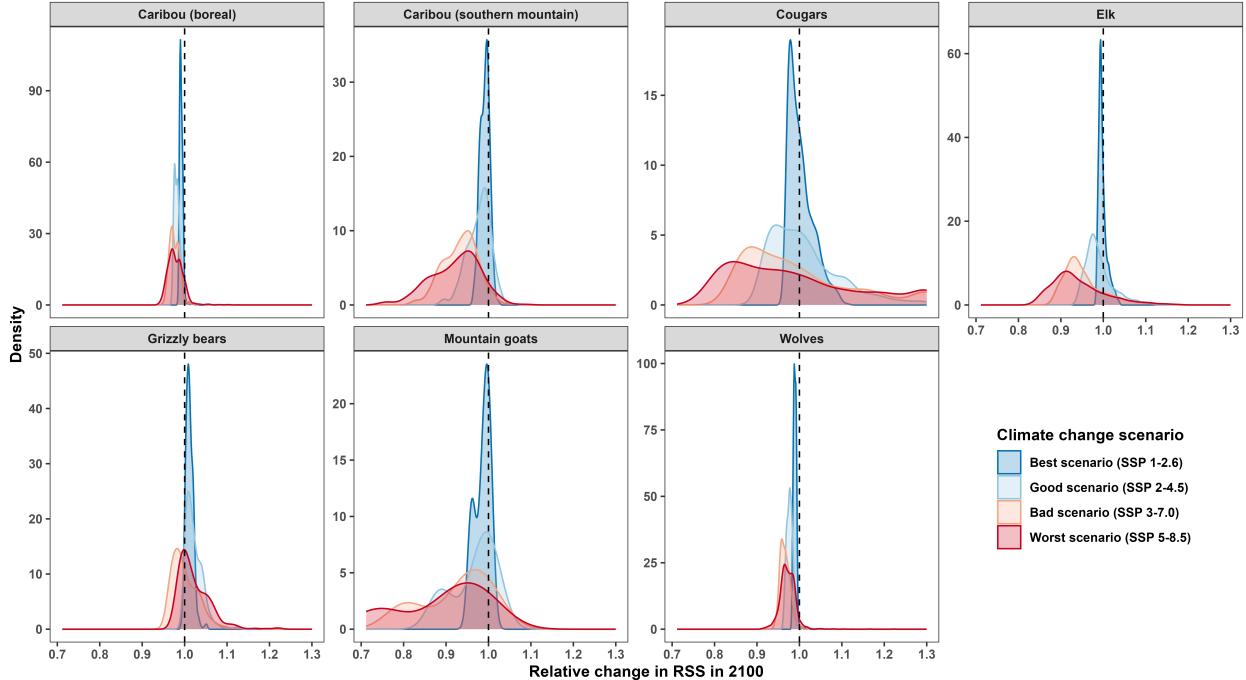


Figure 10: Climate change is predicted to cause species to decrease their selection strength for their current habitats, and worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each 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 crucial for estimating smooth, nonlinear changes in daily and seasonal trends with tem-  
 386 perature with data from multiple individuals. By allowing interaction terms to be smooth  
 387 bivariate functions, we were able to quantify changes in movement behaviour without the  
 388 need to discretize time into windows (e.g., day/night and seasons). We were thus able to  
 389 present results using relatively simple and interpretable surface plots (Figs. 3 and 4) that  
 390 conveyed nuanced, continuous-time estimates of change. This framework was essential for  
 391 estimating how mammals behave at extreme temperatures. In fact, despite the recent in-  
 392 crease in frequency of extreme heat events in western Canada, including a severe heat wave  
 393 in 2021 (Kienzle, 2018; Thompson *et al.*, 2022; Zhang *et al.*, 2023), such events remain rela-  
 394 tively rare, so estimating mammals’ nonlinear responses required the flexibility provided by  
 395 HGAMs (Wood, 2017). Additionally, the hierarchical approach allowed us to leverage data  
 396 from multiple individuals in a single model while accounting for differences in behaviour and  
 397 data availability across individuals (Pedersen *et al.*, 2019; Muff *et al.*, 2020; McCabe *et al.*,

398 2021; Jeltsch *et al.*, 2025; Silva *et al.*, 2025). Still, GAMs' flexibility and complexity can be  
399 a frustrating limitation if used too generously, so we suggest choosing each smooth term's  
400 basis size ( $k$ ) carefully. While penalized splines and REML can help avoid unruly smooth  
401 terms, the penalty terms can struggle to restrict model complexity when datasets are as  
402 large as those presented here (Wood, 2017; Wood *et al.*, 2017).

403 The effects of warming temperatures on movement rates varied across species, seasons,  
404 and space due to differences in species' behavior and physiology as well as their habitats'  
405 phenology (e.g., the timing of green-up). For boreal caribou, hotter temperatures decreased  
406 movement rates summer but increased them otherwise, mirroring previous studies (Stien *et*  
407 *al.*, 2012; Leclerc *et al.*, 2021; Lessard *et al.*, 2025). The increase in movement rates with  
408 temperature during the cold months is likely partly due to shallower snow depth, which  
409 results in greater mobility (Pedersen *et al.*, 2021), but warmer temperatures during snowy  
410 seasons also increase the risk of rain-on-snow events, which limit forage availability and  
411 increase time spent foraging (Stien *et al.*, 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025).  
412 The reduced movement rates during warmer summers are likely mainly due to more frequent  
413 resting and use of thermal refugia, given ungulates' elevated risk of hyperthermia (Alston  
414 *et al.*, 2020; Verzuh *et al.*, 2023). Therefore, although we predict that boreal caribou's  
415 yearly average movement rates will remain approximately unchanged throughout the 21<sup>st</sup>  
416 century, the projections do not show the changes in seasonal movement phenology. This is an  
417 important caveat, since the effects of extreme temperatures are exacerbated by phenological  
418 mismatches with seasonal photoperiod (Walker *et al.*, 2019), including the timing of molting  
419 and reproduction. Earlier growth seasons in boreal and arctic regions have resulted in lower  
420 calf birth and survival (Post & Forchhammer, 2008), while the lengthening of the growth  
421 season has allowed moose (*Alces alces*) and deer to encroach on boreal caribou habitat and  
422 increase the density of coyotes (*Canis latrans*), cougars, and wolves (Barber *et al.*, 2018;  
423 DeMars *et al.*, 2023), whose movement behaviour also depends on ambient temperature.

424 Boreal wolves responded to temperature similarly to boreal caribou, and habitat selec-

425 tion strength was not projected to change noticeably by 2100, but wolves were predicted  
426 to move less in future decades. In contrast, cougars showed markedly different seasonal  
427 responses to temperature, with warmer temperatures always resulting in less travel, which  
428 resulted in strong predicted decreases in movement rates over the 21<sup>st</sup> century. However,  
429 spatial heterogeneity in habitat, climate, and cougar behaviour may cause boreal individuals  
430 to respond to temperature differently from those in our study. Still, rising temperatures  
431 clearly affect more than each individual species' movement behaviour; they have complex  
432 and interconnected effects on entire communities and their trophic structures.

433 Cunningham *et al.* (2021) discuss the importance of adopting a community-level per-  
434 spective when assessing the effects of climate change on animals' movement behaviour and  
435 phenology. For example, as temperatures warm and both boreal caribou and wolves in-  
436 crease their movement rates in fall, winter, and spring, they also increase their encounter  
437 rates (Martinez-Garcia *et al.*, 2020), which will likely increase predation risk when caribou  
438 are pregnant or with young calves. Additionally, while both species saw reduced movement  
439 rates during hot summer days, boreal wolves' use of anthropogenic linear features (e.g., roads,  
440 seismic lines) may allow them to reduce the total thermal costs of movement by moving for  
441 shorter periods while increasing the chances of encountering heat-stressed prey (Whittington  
442 *et al.*, 2011; Dickie *et al.*, 2017; Dickie *et al.*, 2022). Furthermore, caribou that attempt to  
443 reduce predation risk from wolves by avoiding wolf habitat may still risk increasing predation  
444 pressure from bears, cougars, and coyote (Leblond *et al.*, 2016; DeMars *et al.*, 2023; Labadie  
445 *et al.*, 2023).

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

452 energetic costs of movement (White, 2025) and encounter rates with predators (Sullender *et*  
453 *al.*, 2023). However, milder temperatures can also increase plant growth, which allows goats  
454 to spend more time foraging within and less time travelling across patches (Charnov, 1976;  
455 White *et al.*, 2025). Therefore, figure 3 illustrates an estimate of the total effects of temper-  
456 ature on each species' movement rates, but it does not explicitly account for energetic costs.  
457 Similarly, species' changes in habitat selection do not explicitly account for any changes in  
458 physiological or energetic costs. Additionally, forest cover, elevation, and distance from water  
459 are often correlated, so the estimated effects should be interpreted carefully, and they may  
460 not be applicable outside the study areas used here. For example, both mountain goats and  
461 elk selected for higher elevation as temperatures warmed, but our models did not account  
462 for differences in forage availability at different elevations.

463 Climate change has also had extensive impacts on plant growth and phenology (Cleland *et*  
464 *al.*, 2007; Denny, 2019; Tysor, 2025) with consequences on herbivores' behaviour and fitness  
465 (Post & Forchhammer, 2008; Aikens *et al.*, 2017). Additionally, plants' limited ability to  
466 disperse to and establish in new habitats is often a limiting factor for herbivores' ability to  
467 escape hotter temperatures by moving to higher altitudes or latitudes, and the advance of  
468 herbivores can further limit plants' ability to establish (Speed *et al.*, 2012; Diffenbaugh &  
469 Field, 2013). Consequently, mammals that move to higher elevations may be forced to spend  
470 more time foraging (Mezzini *et al.*, 2025), which will increase both their energetic expenditure  
471 and encounter rates with predators and competitors (Kohl *et al.*, 2019; Martinez-Garcia *et*  
472 *al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local peaks become unsuitable  
473 habitat, and moving to nearby higher peaks requires traveling across low-quality and high-  
474 risk habitat (Figure 9), habitat fragmentation may prevent movement across ranges (White  
475 *et al.*, 2025).

476 Growing evidence suggests that mammals' exposure, sensitivity, and adaptability to cli-  
477 mate change will limit their ability to adapt to change (Ameca y Juárez *et al.*, 2012; Diffen-  
478 baugh & Field, 2013). Exposure to warming temperatures is widespread throughout western

479 Canada (Bunnell *et al.*, 2011; Kienzle, 2018; Eum *et al.*, 2023), and changes in temperature  
480 and phenology may be too rapid for many species to respond to (Diffenbaugh & Field, 2013).  
481 Species' adaptability is further challenged by the difficulty in responding to concurrent, mul-  
482 tifarious, and interconnected changes (Diffenbaugh & Field, 2013; Polazzo *et al.*, 2024). In  
483 the future, landscapes may thus become unable to support species and population sizes they  
484 supported historically, and species may begin selecting against historical ranges (Williams  
485 & Blois, 2018). Therefore, it is crucial for conservationists to distinguish between a species'  
486 ideal environmental space and its best available geographic space (*sensu* Matthiopoulos,  
487 2022).

488 Accelerating multifarious change in species' movement behaviour and energetic costs re-  
489 quire conservation measures that are proactive and anticipate future changes. Polazzo *et al.*  
490 (2024) present a framework for estimating species' responses to multifarious change using  
491 GAMs that is particularly useful when estimating species' (nonlinear) responses to inter-  
492 actions between environmental variables (e.g., changes in both temperature and limiting  
493 nutrients). By accounting for the effects of multiple variables at once, they demonstrate  
494 how a species' response to one variable can depend on other concurrent changes. Estimat-  
495 ing responses to multifarious change is crucial in assessing mammals' responses to hotter  
496 temperatures, altered phenology, and novel community dynamics.

497 Protected areas must support populations not only in present conditions but also as  
498 species' needs and behaviour change over the decades (Simmons *et al.*, 2021; Livingstone *et*  
499 *al.*, 2023). Recent evidence has questioned whether current protected areas will be effective  
500 in the long term (Loarie *et al.*, 2009; Diffenbaugh & Field, 2013; Williams & Blois, 2018),  
501 and increasingly more experts have been calling for proactive and long-term conservation.  
502 By identifying and actively protecting climate change refugia and corridors, we may be able  
503 to reduce the effects of climate change on mammalian movement behaviour and community-  
504 level responses and ensure that protected areas may be viable for decades to come (Michalak  
505 *et al.*, 2018; Graham *et al.*, 2019; Stralberg *et al.*, 2020; Hua *et al.*, 2022).

506 Future work should develop models that account for covariates that are specific to the  
507 study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain  
508 ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),  
509 and growing human presence in wild spaces (Sih *et al.*, 2011; Rice, 2022), including the  
510 growing risk of human-wildlife conflict (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In  
511 particular, forests in western Canada are highly dynamic over time (Zhang *et al.*, 2015), and  
512 fires size and burn severity have increased in western Canada in recent decades (Whitman *et*  
513 *al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025). Thus, while our use of a static raster of  
514 forest cover allowed for simpler models and climate change projections, future studies should  
515 account for mammals' responses to temporal forest dynamics, including the impacts of fire  
516 (Whitman *et al.*, 2022; Parisien *et al.*, 2023; Wang *et al.*, 2025), logging (Lochhead *et al.*,  
517 2022) and other extractive industries (Dickie *et al.*, 2017, 2024). However, the inclusion of  
518 temporally dynamic variables will require that any future projections of species' behaviour  
519 depend on temporally dynamic estimates of how such variables will change over time with  
520 changes in climate and anthropogenic activity.

521 We have demonstrated that temperature has complex and nonlinear effects on how and  
522 where boreal mammals move. Rising temperatures have impacted mammals' daily and sea-  
523 sonal movement cycles, and changes are expected to intensify throughout the 21<sup>st</sup> century.  
524 Quantifying how temperature affects mammalian behavior and fitness is a first step towards  
525 developing an understanding of the effects of climate change on landscape dynamics and the  
526 effectiveness of protected areas in the future. By leveraging the flexibility and statistical  
527 power of Hierarchical Generalized Additive Models, we have provided researchers with mal-  
528 leable and data-driven methods for assessing species' responses to climate change. We hope  
529 that future work will develop more species-specific models with the intent of developing a  
530 community-level framework for quantifying and predicting how communities will respond to  
531 climate change.

<sup>532</sup> **Author contributions**

<sup>533</sup> SM performed the data cleaning, ran the analyses, and wrote the manuscript. CHF wrote  
<sup>534</sup> code for estimating instantaneous movement speeds. MJN conceived of the project idea and  
<sup>535</sup> supervised SM throughout the project. All other authors contributed telemetry data and  
<sup>536</sup> reviewed the interpretation of the results for their species of interest. KH and SD contributed  
<sup>537</sup> substantially to manuscript review. All authors contributed to reviewing the manuscript.

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