

# 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 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 of how and where these mammals moved, and we predict that climate change will impact mammals' movement behaviour throughout the 21<sup>st</sup> century, although species did not respond uniformly to temperature. 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 seasonal phenology. We also predict that rising temperatures will reduce median habitat selection strength most of the six species, but some 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. Proactively 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 *et*  
<sup>14</sup> *al.*, 2022), and life history (Newediuk *et al.*, 2024), and even cause physiological damage and  
<sup>15</sup> death (Heten *et al.*, 2014; Powers *et al.*, 2017; Ratnayake *et al.*, 2019; Schmidt *et al.*, 2020;  
<sup>16</sup> Schwerdt *et al.*, 2024). Animals may search for a short-term buffer from extreme tempera-  
<sup>17</sup> tures by moving to thermal refugia (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*,  
<sup>18</sup> 2018; Arechavala-Lopez *et al.*, 2019; Gulland *et al.*, 2022), and shelter may even be preferred  
<sup>19</sup> over forage abundance (Hall *et al.*, 2016). However, climate change during the last century  
<sup>20</sup> (IPCC, 2023) have caused animals to alter how and where they move as they respond to  
<sup>21</sup> hotter temperatures and increasingly severe and frequent extreme-heat events (Bunnell *et*  
<sup>22</sup> *al.*, 2011; 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. Large-bodied mammals are most 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). Global  
34 warming during the last century has resulted in milder and shorter winters, hotter and longer  
35 summers, and a greater risk of extreme-heat events (IPCC, 2023), with widespread changes  
36 in mammals' seasonal phenology, fitness, and life history (Botero *et al.*, 2015; McLellan &  
37 McLellan, 2015; Pigeon *et al.*, 2016; Wells *et al.*, 2022; Newediuk *et al.*, 2024). However,  
38 behavioural responses to heat vary substantially across species depending on body size,  
39 vagility, and activity times (McCain & King, 2014; Williams & Blois, 2018). For example,  
40 warming temperatures have allowed deer (*Odocoileus* spp.) to shift northward, which has  
41 led to increased density of wolves (*Canis lupus*) and higher predation on caribou (*Rangifer*  
42 *tarandus caribou*) (Latham *et al.*, 2011; Barber *et al.*, 2018; Dickie *et al.*, 2024). Preparing  
43 for and responding to future changes will require a detailed understanding of not only how  
44 how and where mammals move throughout the thermal landscape but also the cascade of  
45 effects that such changes will have at the population and community levels (Cunningham *et*  
46 *al.*, 2021).

47 As heat stress intensifies over the next 100 years, mammals will continue to suffer impacts  
48 on their fitness, movement rates, and habitat selection (Deb *et al.*, 2020; Woo-Durand *et*  
49 *al.*, 2020). It remains unclear how or whether species will be able to respond to climate  
50 change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*,  
51 2023), especially if populations fail to adapt (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are  
52 physiologically incapable to do so (Sherwood & Huber, 2010; Botero *et al.*, 2015; Williams  
53 & Blois, 2018). Recent work has documented the effects of climate change on mammals'

54 ranges (Leclerc *et al.*, 2021), thermoregulation (Mota-Rojas *et al.*, 2021), and movement  
55 behaviour (McCain, 2019; Cunningham *et al.*, 2021; Melin *et al.*, 2023), but there remains a  
56 need for fine-scale estimates of the effects of temperature on mammals' movement behaviour  
57 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: *Canis lupus*; Table 1). Western Canada is currently  
63 experiencing accelerating and widespread but spatially heterogeneous warming (Turner &  
64 Clifton, 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu  
65 *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme heat events (Zhang *et*  
66 *al.*, 2023). Decision makers must understand which areas will best sustain and protect bio-  
67 diversity not only for current conditions but future decades, too. Failing to understand  
68 how climate change will affect mammalian movement behaviour will hinder our ability to  
69 respond to the current climate crisis and make decisions that are viable in the long term.  
70 Furthermore, understanding how temperature affects individual species is the first step to-  
71 wards understanding how temperature impacts the community dynamics (Hegel *et al.*, 2010;  
72 Cunningham *et al.*, 2021; Carbeck *et al.*, 2022) and habitat phenology (Bunnell *et al.*, 2011;  
73 Duncan *et al.*, 2012; Merkle *et al.*, 2016; Slatyer *et al.*, 2022; Gerlich *et al.*, 2025), and how  
74 these changes will impact mammals in the coming decades (Sobie *et al.*, 2021; Eum *et al.*,  
75 2023; Weststrate *et al.*, 2024). We discuss the consequences of our findings at the individual,  
76 population, and community levels, and we also provide directions for future research and  
77 solutions for overcoming some common data limitations.

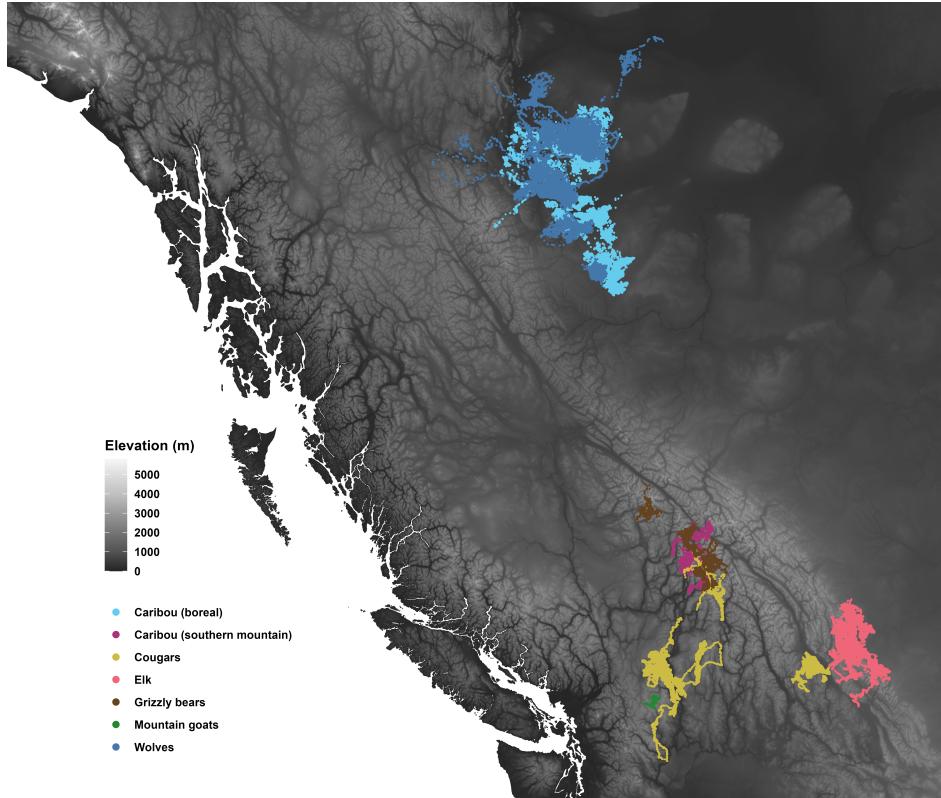


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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

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

78 **2 Methods**

79 **2.1 Datasets used**

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

93 We acknowledge that our models of habitat selection ignore many important variables of  
94 habitat selection (e.g., forest type, structure, and age; terrain slope and aspect; prey avail-  
95 ability; population density). We limited our models to only use three simple and temporally  
96 static rasters to produce simple and easily interpretable estimates and forecasts under the  
97 assumption of temporally invariant landscapes. See the discussion section for additional  
98 detail on the advantages and limitations of using such simple models.

99 **2.1.1 GPS telemetry data**

100 Boreal caribou and wolf telemtries were acquired from a data repository of the British  
101 Columbia Oil and Gas Research and Innovation Society (BC ORGIS) that was collected as  
102 part of the boreal caribou radio-collaring program of the BC OGRIS Research and Effective-

ness Monitoring Board (REMB; BC OGRIS, 2018). Southern mountain caribou data were obtained from the work of Ford *et al.* (2023). Cougar data include telemetries from Darlington *et al.* (2025) and (*serrouya\_ref?*). Elk data from the work of Ciuti *et al.* (2012) were downloaded from Movebank (Kays *et al.*, 2022). ***MISSING INFO ON GRIZZLY BEAR AND GOAT TELEMETRY DATA.***

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

### 2.1.2 Historical temperature data and climate change projections

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

To obtain projected average monthly temperatures from 2025 to 2100 at a  $0.08^\circ$  spatial resolution, we used the `climatenaR` package (v. 1.0, Burnett, 2023) for R and ClimateNA v. 7.4.2 (Wang *et al.*, 2016; Mahony *et al.*, 2022). However, the climate projections only 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

129 1998 to 2023 (inclusive). For each location  $\langle x, y \rangle$  and month  $m$  of each year (e.g., the  
 130 observed variance at coordinates  $\langle -119.40, 49.94 \rangle$  in April 2005), we calculated the variance  
 131 in historical temperature data, for a total of  $(2024 - 1998) \times 12 = 312$  observations per  
 132 location. We then modeled  $\sigma_T^2$  a Generalized Additive Model (GAM) for Location and Scale  
 133 (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood,  
 134 2017) fitted with the `mgcv` package for R (v. 1.9-1, Wood, 2017). The linear predictor  
 135 for the location (i.e., the mean) included smooth terms of: each year's estimated within-  
 136 pixel monthly mean temperature ( $\hat{\mu}_T$ ), month ( $m$ ), a two-dimensional smooth of spatial  
 137 coordinates  $\langle x, y \rangle$ , and a tensor product interaction term of month and space to allow for  
 138 seasonal terms to vary smoothly over space. The linear predictor for the scale term, which  
 139 governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included smooth  
 140 terms of the monthly mean temperature, month, and space. We did not include smooth terms  
 141 of year to avoid unrealistic projections when extrapolating beyond past 2023. The complete  
 142 model for the distribution of projected temperature was thus

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

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

<sup>147</sup> December and January, the terms use cyclic cubic spline bases. The spatial terms used two-  
<sup>148</sup> dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood  
<sup>149</sup> (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood  
<sup>150</sup> (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information  
<sup>151</sup> on the code used to fit the model.

<sup>152</sup> We simulated hourly variation in future years by assuming hourly temperature followed  
<sup>153</sup> a normal distribution with mean specified by the monthly `climatenar` climate projections  
<sup>154</sup> and variance as specified by the gamma GMLS. For each month within each year from  
<sup>155</sup> 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the  
<sup>156</sup> 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the  
<sup>157</sup> (normalized) Gaussian probability density for each quantile.

### <sup>158</sup> 2.1.3 Habitat rasters

<sup>159</sup> We estimated percent forest cover and distance from water using the temporally static  
<sup>160</sup> rasters created by Tuanmu & Jetz (2014). We calculated total forest cover by summing  
<sup>161</sup> the four rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, decidu-  
<sup>162</sup> ous broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted  
<sup>163</sup> the raster of percent cover of open water (class 12) to a binary raster of pixels with water  
<sup>164</sup> ( $\text{cover} > 0\%$ ) or without water ( $\text{cover} = 0\%$ ) and then calculated each pixel's distance from  
<sup>165</sup> the nearest pixel with water using the `distance()` function from the `terra` package. Fi-  
<sup>166</sup> nally, we obtained two digital elevation models using the `get_elev_raster()` function from  
<sup>167</sup> the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom of 6  
<sup>168</sup> (a resolution of  $0.009^\circ$ ) for model fitting and one with a zoom of 3 (a resolution of  $0.08^\circ$ )  
<sup>169</sup> for downloading climate change projections via `climatenar`. All final rasters and code are  
<sup>170</sup> available on GitHub (see the Data Availability Statement). For ease of interpretability and  
<sup>171</sup> comparison with current conditions, we assumed resources would remain constant through  
<sup>172</sup> to 2100, although we recognize that the spatial distribution of forest cover and open water

<sub>173</sub> will likely change throughout the 21<sup>st</sup> century.

<sub>174</sub> **2.2 Estimating mammals' instantaneous speeds**

<sub>175</sub> We modeled each animal's movement using continuous-time movement models (Fleming  
<sub>176</sub> *et al.*, 2014) via the `ctmm` package (v. 1.2.0, Fleming & Calabrese, 2023) for R. We then  
<sub>177</sub> estimated each mammal's instantaneous speed at each observed location by applying the  
<sub>178</sub> `ctmm::speeds()` function on all models with finite speed estimates (415 of 433, Fleming *et*  
<sub>179</sub> *al.*, 2014; Noonan *et al.*, 2019a). The 18 animals with insufficiently fine sampling to support  
<sub>180</sub> movement models with finite speed were for one mountain goat, 15 boreal caribou, and two  
<sub>181</sub> southern mountain caribou (Table 1).

<sub>182</sub> Since `ctmm`'s movement models assume a single moving state with stochastic but non-zero  
<sub>183</sub> speed (Calabrese *et al.*, 2016; Noonan *et al.*, 2019a), we corrected data-informed speeds so  
<sub>184</sub> that the minimum instantaneous speed could be 0. We performed this correction by sub-  
<sub>185</sub> tracting each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function  
<sub>186</sub> we used is available on GitHub (see the Data Availability Statement). To avoid artifacts  
<sub>187</sub> due to excessively small, non-zero speeds, we determined whether an animal was moving or  
<sub>188</sub> not using a *k*-means algorithm with 2 clusters for each species' distribution of detrended  
<sub>189</sub> speeds. When the algorithm clearly failed to discriminate between states, we estimated the  
<sub>190</sub> split point using the inflection points in histograms of the detrended speeds (Fig. B1).

<sub>191</sub> **2.3 Estimating the effects of temperature on mammals' movement behaviour**

<sub>192</sub> Ambient temperature is only one of the many drivers of mammalian movement behaviour  
<sub>193</sub> (Fig. 2). Many species alter their movement rates (e.g., movement frequency and speed)  
<sub>194</sub> daily or seasonally in response to factors such as solar time, photoperiod, forage availability,  
<sub>195</sub> reproductive cycles, and predator avoidance. Similarly, ambient temperature also fluctuates  
<sub>196</sub> throughout the day and across seasons. Therefore, estimating the effects of temperature  
<sub>197</sub> on movement rates requires accounting for how mammals' response to temperature changes

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

203 To assess the importance of including temperature as an explicit covariate (as opposed  
 204 to including its effects with time of day and day of year), we fit models with and without  
 205 smooth effects of temperature and compared the fits of the two sets of models via analyses  
 206 of deviance (a form of generalized likelihood ratio tests) following the methods of Section  
 207 3.3 in Wood (2017). See Appendix B for additional information.

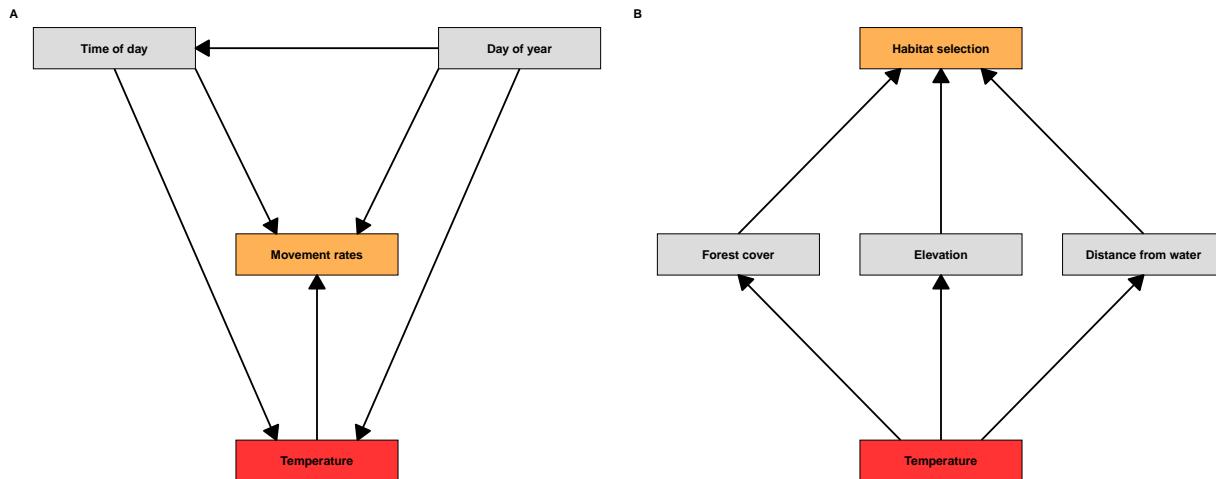


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

### 208 2.3.1 Effects of temperature on movement rates

209 We estimated the effects of temperature on mammals' instantaneous movement state (mov-  
 210 ing or not) and speed when moving using two Hierarchical Generalized Additive Models

(HGAMs; 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 al.*, 2019). The `by` smooths accounted for trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). To account for the cyclicity of time of day and day of year, the smooth terms used cyclic cubic splines (p. 202 of Wood, 2017). The models also had three tensor product interaction terms `by` each species: (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and day of year. These three terms accounted for smooth changes in: (1) daily behaviour across day of year, (2) the response to temperature over time of day (e.g., changes in nocturnality), and (3) the response to temperature over day of year (e.g., the timing of molting, migration, and hibernation). Finally, two smooth terms of log-transformed sampling interval (`dt`; hours) corrected for biases in speed estimates arising from irregular GPS sampling intervals, since longer intervals result in lower speed estimates (Nathan *et al.*, 2022; DeNicola *et al.*, 2025). A global smooth term of  $\log(dt)$  accounted for the overall effect of sampling interval, while a factor-smooth interaction term (`bs = 'fs'`) of  $\log(dt)$  and species accounted for species-level deviations from the global term while assuming a common smoothness parameter across species (model GS in Figure 4 of Pedersen *et al.*, 2019). Formally, the model for movement

<sup>238</sup> state  $M$ , with  $M = 0$  indicating no movement and  $M = 1$  indicating movement, was

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

<sup>239</sup> while the model for movement speed when moving (i.e.,  $M = 1$ , indicated with  $S$ ) was

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

<sup>240</sup> In both models,  $\beta_s$  indicates a fixed intercept for species  $s$ ,  $Z_a$  indicates a Gaussian random  
<sup>241</sup> effect for animal  $a$  (of species  $s$ ),  $f_{j,s}$  indicates the  $j^{\text{th}}$  smooth function for species  $s$ , and  
<sup>242</sup> functions with two variables indicate tensor product interaction terms. The model code used  
<sup>243</sup> to fit the models is available in Appendix B.

<sup>244</sup> **2.3.2 Effects of temperature on habitat selection**

<sup>245</sup> We estimated the effects of temperature on each species' selection for percent forest  
<sup>246</sup> cover (`forest_perc`), elevation (`elevation_m`, in meters), and distance from water  
<sup>247</sup> (`dist_water_m`, in meters) by fitting a Hierarchical Resource Selection Function (HRSF) for  
<sup>248</sup> each species (McCabe *et al.*, 2021). We fit each HRSF using an HGAM with a Poisson family  
<sup>249</sup> of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After removing  
<sup>250</sup> non-resident individuals (Table B1), we accounted for the spatiotemporal autocorrelation  
<sup>251</sup> in the telemetry locations by weighting each point based on the telemetry's Autocorrelated  
<sup>252</sup> Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b; Alston *et al.*,  
<sup>253</sup> 2022) to produce estimates of second-order habitat selection (Johnson, 1980). Quadrature  
<sup>254</sup> points were used to approximate the likelihood function of a Poisson point process through  
<sup>255</sup> Monte-Carlo Markov chain-based integration (Aarts *et al.*, 2008; Fithian & Hastie, 2013;  
<sup>256</sup> Baddeley *et al.*, 2015) and were determined using the raster cells in each animal's 99.9%  
<sup>257</sup> AKDE percentile, with each raster cell having a weight of 1. The number of quadrature  
<sup>258</sup> locations greatly outnumbered the number of observed locations (Fig. B12), especially after  
<sup>259</sup> accounting for the AKDE weights (Fig. B13).

<sup>260</sup> Each species' model had the same structure:

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

<sup>261</sup> 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). Consequently, we present all results while predicting specifically for one-hour sampling intervals. At  $0^{\circ}\text{C}$ , species differed in estimated mean probabilities of moving ( $\hat{P}(M = 1)$ ; range:  $0.05 - 0.31$ ), mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1)$ ; range:  $0.42 - 2.67 \text{ km/h}$ ), and mean distance traveled (i.e.,  $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$ , range:  $0.04 - 0.61 \text{ km/h}$ ; 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 ( $\hat{\mathbb{E}}(S|M = 1) \approx 0.43 \text{ km/h}$ ), while wolves had the highest mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1) \approx 2.67 \text{ km/h}$ ). Consequently, at  $0^{\circ}\text{C}$ , wolves traveled an average of  $0.22 \times 2.67 \text{ km/h} \approx 0.6 \text{ km/h}$ ; 2.5 to 16.7 times further than other species.

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

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

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

299 There was relatively strong agreement between models with and without temperature  
 300 (Figs. B3, and B14), but including temperature always resulted in better fits (all p-values  
 301  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \leq -342$ ; Appendix B). Accounting for temperature even resulted in  
 302 a simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better  
 303 (lower deviance), and hence no test was necessary to show that the inclusion of temperature

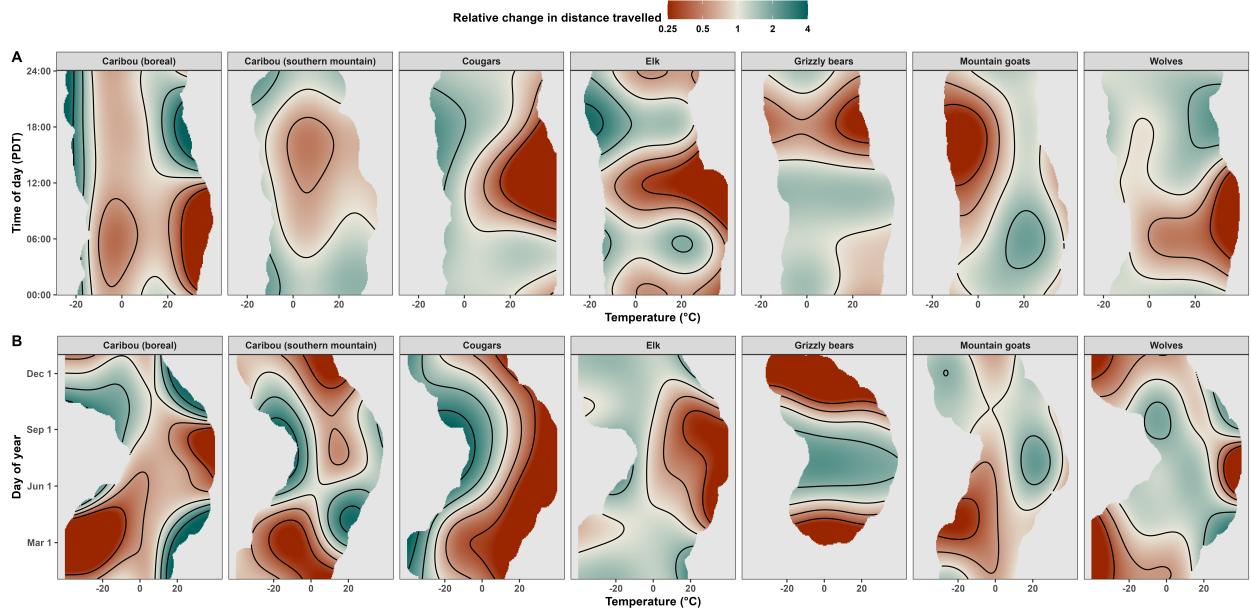
304 produced a better fit.

305 **3.1 Effects of temperature on movement rates**

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

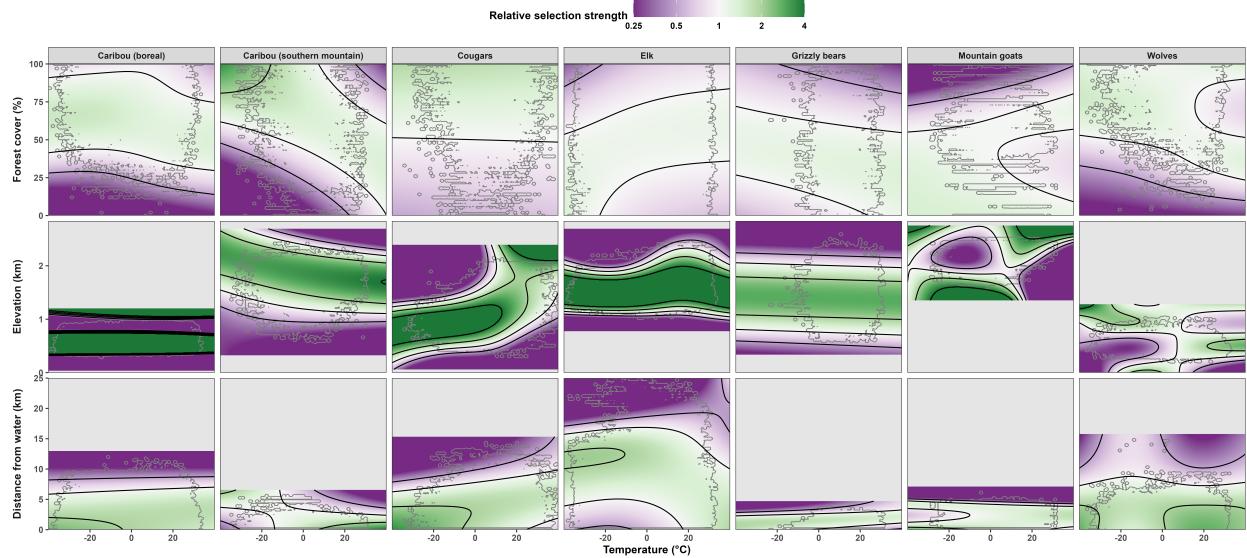
322 **3.2 Effects of temperature on habitat selection**

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



**Figure 3: Temperature is a strong driver of how far and when mammals travel.** The fill indicates the effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year at 12:00 PDT (**B**). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the  $\log_2$  scale to help visualize patterns in doubling, and values are capped to  $2^{\pm 2}$  for ease of readability.

their preference for forested areas, while mountain goats relaxed their preference open areas (cover < 50%). As temperatures warmed, elk and boreal caribou shifted towards more forest cover closer to 50%, while southern mountain caribou and grizzly bears selected for areas with 50% forest cover or less. All species shifted elevationally with temperature, although boreal caribou had a much sharper change in RSS across elevation. Elk, mountain goats, and cougars moved to higher elevations with temperature, while wolves, southern mountain caribou, and grizzly bears moved to lower elevations. Wolves, elk, and southern mountain caribou moved closer to water with temperature, while mountain goats, cougars, and grizzly bears moved somewhat further away from water but remained mainly within 5-10 km of water. As with movement rates, estimated RSS was generally most uncertain at extreme temperatures, for which data was scarcer (Fig. B15).



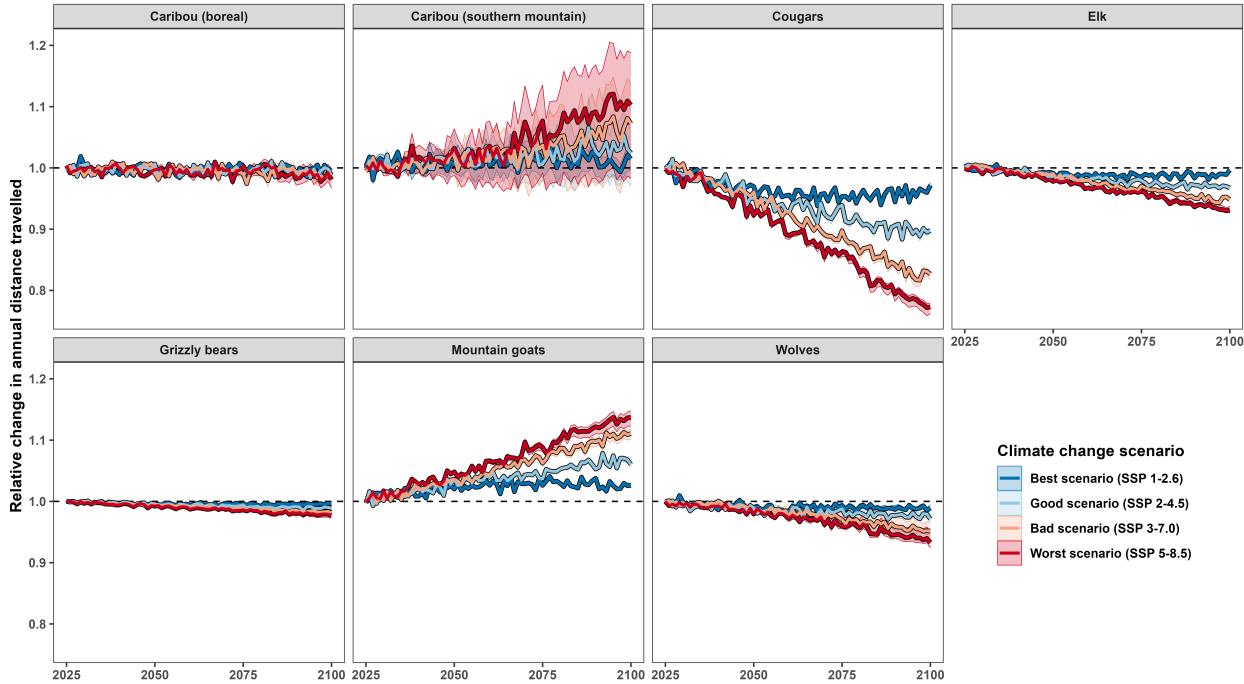
**Figure 4: Mammals’ habitat selection depends on ambient temperature.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species’ observed data. RSS values were re-centered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

### 340 3.3 Predicted changes in movement behaviour during the 21<sup>st</sup> century

341 Predicted changes in movement rates with future climate change varied across species in both  
 342 magnitude and direction, but worse SSPs always corresponded to greater absolute changes  
 343 (Fig. 5). Additionally, species that were predicted to move less often did not necessarily  
 344 have lower speeds when moving, and vice versa (Figs. B9 and B10). Estimated changes  
 345 in average distance traveled were negligible for boreal caribou, and grizzly bears, although  
 346 both species showed seasonal changes in seasonal movement rates. As temperatures warmed,  
 347 boreal caribou moved further in winter, spring, and fall but less in summer, while grizzly  
 348 bears showed a clear shift towards earlier emergence from hibernation (Fig. B4) and greater  
 349 movement earlier in the year but less movement in early fall. Southern mountain caribou  
 350 and mountain goats are projected to travel further by 2100, although the estimates for  
 351 southern mountain caribou varied greatly over space (Fig. 6). Cougars, elk, and wolves were  
 352 projected to move less by 2100, with cougars showing as much as a 24% decrease in mean  
 353 yearly distance travelled.

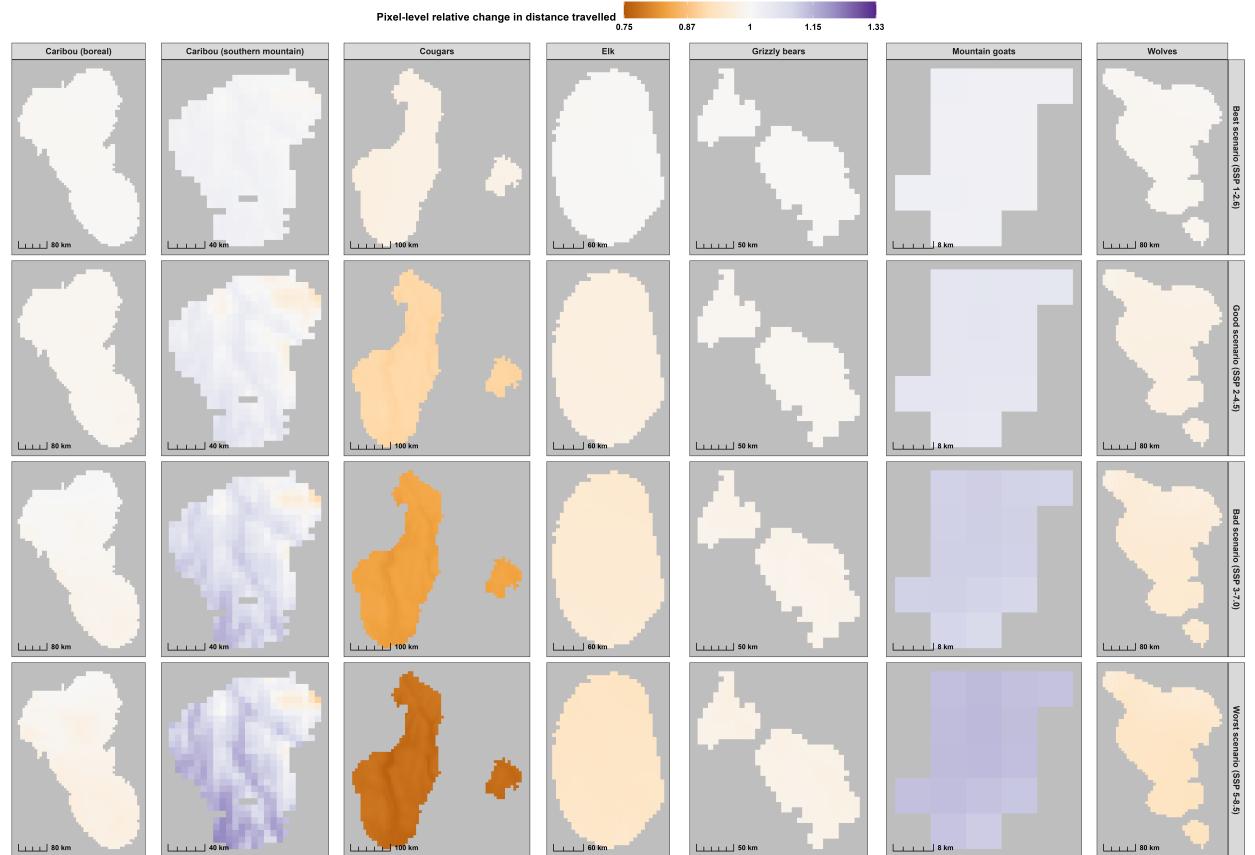
354 Absolute relative changes in average yearly distance travelled were small under the best-

case SSP (0-4% change in 2100 relative to 2025). Under the worst-case SSP, absolute changes by 2100 (relative to 2025) ranged from ~2% (grizzly bears) to ~24% (cougars). Projected changes in 2100 varied spatially due to spatial heterogeneity in climate change projections (Fig. 6). Again, absolute changes were generally greatest under worse SSPs, but the direction of change at each location also varied across SSPs (most visible in cougars).



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

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



**Figure 6: Climate change will impact each species' movement rates differently, but changes will also vary spatially.** The color of each pixel indicates the predicted changes in distance traveled in 2100 at that pixel, relative to the value in 2025, averaged across all four scenarios. Values  $< 1$  indicate a decrease, and values  $> 1$  indicate an increase. For ease of readability, the color bar is on the  $\log_2$  scale to help visualize patterns in doubling). The predictions only account for the predicted temperature throughout the areas and ignore environmental factors such as terrain slope, soil type, and forest density. All maps extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

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

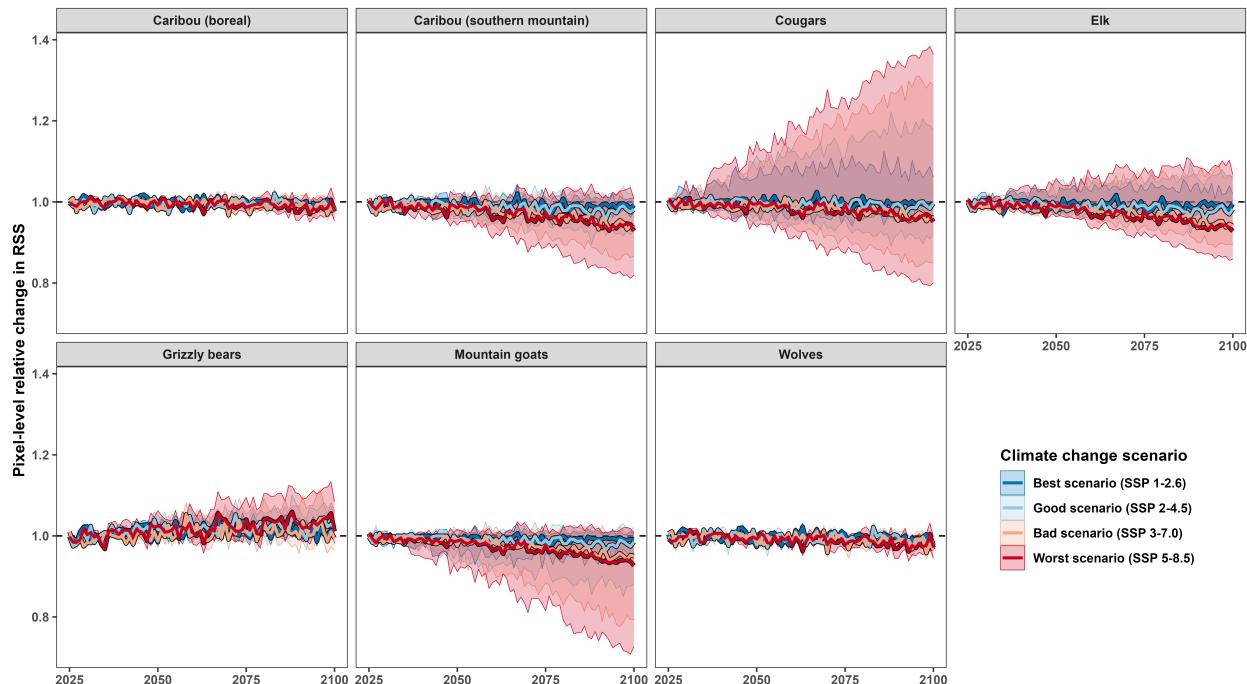


Figure 7: Species will alter their habitat selection differently in response to climate change, but worse climate-change scenarios will result in the greatest change. Bold lines indicate the change in median RSS due to predicted changes in temperature within each species' observed extent. Shaded areas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

## 371 4 Discussion

372 We have demonstrated that temperature is an important driver of how and where large  
 373 mammals move, and that it affects mammals' seasonal and daily movement behaviour in  
 374 complex and nonlinear ways. However, predicting mammals' responses to climate change  
 375 remains a challenge, as habitats are warming rapidly and mammals are exposed to increas-  
 376 ingly novel and extreme conditions (Diffenbaugh & Field, 2013; Botero *et al.*, 2015; IPCC,  
 377 2023). We leveraged the flexibility and interpretability of HGAMs to estimate mammals'



**Figure 8: Climate change will impact each species' relative selection strength (RSS) differently.** The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios (i.e., not relative to other pixels). Values  $< 1$  indicate a decrease and values  $> 1$  indicate an increase. For ease of readability, the color bar is on the  $\log_2$  scale to help visualize patterns in doubling, and values are capped to 0.8 and 1.25 ( $\approx 2^{\pm 0.322}$ ; original data ranged 0.71 to 1.93). All maps extend to each species' observed extent (Fig. 1) and are shown in the BC Albers Equal Area Conic projection (EPSG:3005).

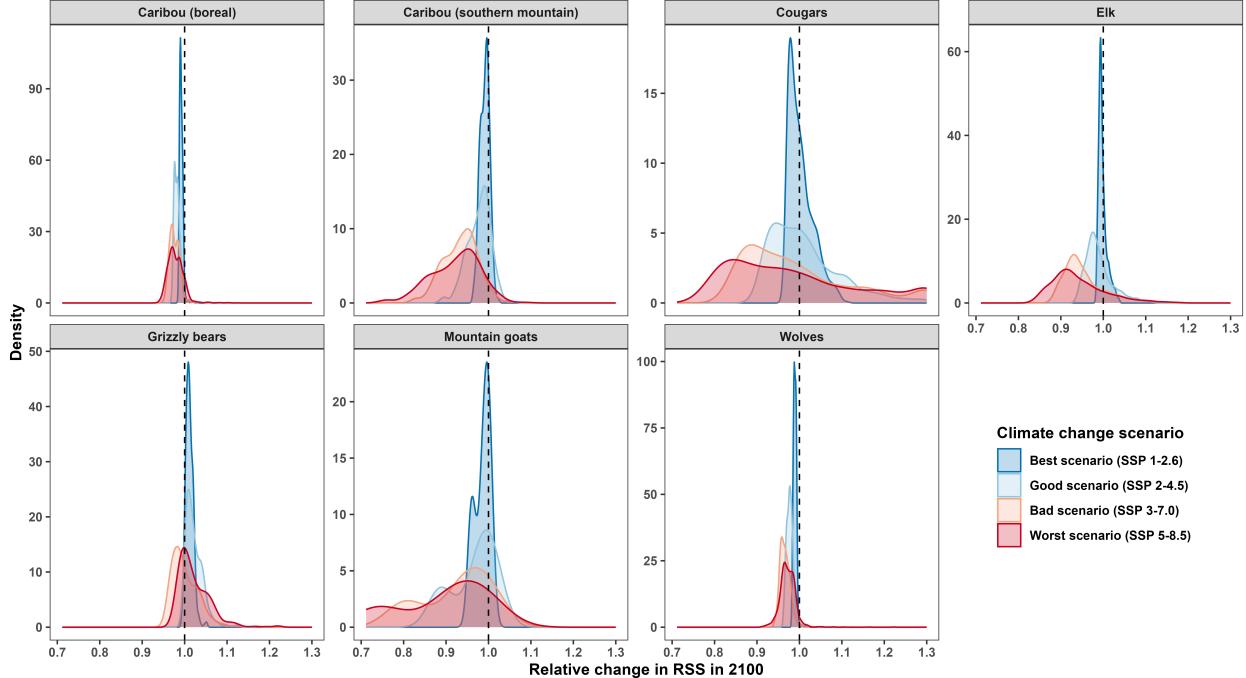


Figure 9: Climate change will cause species to decrease their selection strength for their current habitats, but worse climate change scenarios will have the greatest impact. The density plots indicate each species’ change in RSS in 2100 for their current habitat (Fig. 8), relative to each location’s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

378 nonlinear responses to temperature without imposing rigid assumptions about the shape of  
 379 the responses (Simpson, 2018, 2025). In particular, tensor product interaction terms were  
 380 crucial for estimating smooth, nonlinear changes in daily and seasonal trends with tem-  
 381 perature with data from multiple individuals. By allowing interaction terms to be smooth  
 382 bivariate functions, we were able to quantify changes in movement behaviour without the  
 383 need to discretize time into distinct windows (e.g., day/night and seasons). We were thus  
 384 able to present results using relatively simple and interpretable surface plots (Figs. 3 and 4)  
 385 that conveyed nuanced, continuous-time estimates of change. This framework was essential  
 386 for estimating how mammals behave at extreme temperatures. In fact, despite the recent  
 387 increase in frequency of extreme heat events in western Canada (Bunnell *et al.*, 2011; Kien-  
 388 zle, 2018; Zhang *et al.*, 2023), such events remain relatively rare, so estimating mammals’  
 389 nonlinear responses required the flexibility provided by GAMs (Wood, 2017). Additionally,  
 390 hierarchical models allowed us to produce statistically sound estimates that accounted for

<sup>391</sup> differences in behaviour and data availability across individuals (Pedersen *et al.*, 2019; Muff  
<sup>392</sup> *et al.*, 2020; McCabe *et al.*, 2021; Jeltsch *et al.*, 2025; Silva *et al.*, 2025). Still, GAMs' flex-  
<sup>393</sup> ibility and complexity can be a frustrating limitation if used too generously, so we suggest  
<sup>394</sup> choosing each smooth term's basis size ( $k$ ) carefully. While penalized splines and REML can  
<sup>395</sup> help avoid unruly smooth terms, the penalty terms can struggle to restrict model complexity  
<sup>396</sup> when datasets are particularly large (Wood, 2017; Wood *et al.*, 2017).

<sup>397</sup> Species varied greatly in how they adapted their movement behaviour to temperature.  
<sup>398</sup> For boreal caribou, hotter temperatures increased movement rates in fall, winter, and spring  
<sup>399</sup> but decreased them in summer, mirroring the findings of Stien *et al.* (2012), Leclerc *et al.*  
<sup>400</sup> (2021), and Lessard *et al.* (2025). The increase in movement rates during the colder seasons  
<sup>401</sup> are likely partly due to shallower snow depth that results in greater mobility (Pedersen *et*  
<sup>402</sup> *al.*, 2021), but rising temperatures during snowy seasons also increase the risk of rain-on-  
<sup>403</sup> snow events, which limit forage availability and increase time spent foraging (Stien *et al.*,  
<sup>404</sup> 2012; Berger *et al.*, 2018; Mezzini *et al.*, 2025). The reduced movement rates during warmer  
<sup>405</sup> summers are likely mainly due to more frequent resting and use of thermal refugia, given  
<sup>406</sup> ungulates' elevated risk of hyperthermia (Alston *et al.*, 2020; Verzuh *et al.*, 2023). Therefore,  
<sup>407</sup> although we predict that boreal caribou's yearly average movement rates will remain approx-  
<sup>408</sup> imately unchanged throughout the 21<sup>st</sup> century, the projections do not show the changes in  
<sup>409</sup> seasonal movement phenology. This is an important caveat, since the effects of extreme tem-  
<sup>410</sup> peratures are exacerbated by phenological mismatches with seasonal photoperiod (Walker  
<sup>411</sup> *et al.*, 2019), including the timing of molting and reproduction. Earlier growth seasons in  
<sup>412</sup> boreal and arctic regions have resulted in lower calf birth and survival (Post & Forchhammer,  
<sup>413</sup> 2008), while the lengthening of the growth season has allowed moose (*Alces alces*) and deer  
<sup>414</sup> to encroach on boreal caribou habitat and increase the density of coyotes (*Canis latrans*),  
<sup>415</sup> cougars, and wolves (Barber *et al.*, 2018; DeMars *et al.*, 2023), whose movement behaviour  
<sup>416</sup> also depends on ambient temperature. Boreal wolves responded to temperature similarly  
<sup>417</sup> to boreal wolves, and habitat selection strength was not projected to change noticeably by

418 2100, but wolves were predicted to move less in future decades. In contrast, cougars showed  
419 markedly different seasonal responses to temperature, with relatively warmer temperatures  
420 always resulting in less travel, which resulted in strong predicted decreases in movement rates  
421 over the 21<sup>st</sup> century. However, spatial heterogeneity in habitat, climate, and cougar physi-  
422 ology and behaviour may cause cougars in boreal regions to move differently from those in  
423 our study. Still, rising temperatures clearly affect more than each individual species' move-  
424 ment behaviour; they have complex and interconnected effects on entire communities and  
425 their trophic structures.

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

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

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

456 Climate change has also had extensive impacts on plant growth and phenology (Cleland *et*  
457 *al.*, 2007; Denny, 2019; Tysor, 2025) with consequences on herbivores' behaviour and fitness  
458 (Post & Forchhammer, 2008; Aikens *et al.*, 2017). Forage quality and availability are often  
459 a limiting factor for herbivores' ability to escape hotter temperatures by moving to higher  
460 altitudes or latitudes, since plants are slower to arrive in and establish in new habitats, and  
461 the advance of herbivores can further limit plants' ability to establish (Speed *et al.*, 2012;  
462 Diffenbaugh & Field, 2013). Consequently, mammals that move to higher elevations may  
463 be forced to spend more time foraging (Mezzini *et al.*, 2025), which will increase both their  
464 energetic expenditure and encounter rates with predators and competitors (Kohl *et al.*, 2019;  
465 Martinez-Garcia *et al.*, 2020; Tórrez-Herrera *et al.*, 2020; Smith *et al.*, 2023). If local peaks  
466 become unsuitable habitat, and moving to nearby higher peaks requires traveling across  
467 low-quality and high-risk habitat (Figure 8), habitat fragmentation may prevent movement  
468 across ranges (White *et al.*, 2025). Translocating animals to locations with higher peaks may  
469 help avoid such a scenario, but the success of relocations is species-dependent, and attempts  
470 are not always successful (Ranc *et al.*, 2022; White *et al.*, 2025).

471 Growing evidence suggests that mammals' exposure, sensitivity, and adaptability to cli-

mate change will limit their ability to adapt to change (Ameca y Juárez *et al.*, 2012; Diffenbaugh & Field, 2013). Exposure to warming temperatures is widespread throughout western Canada (Bunnell *et al.*, 2011; Kienzle, 2018; Eum *et al.*, 2023), and changes in temperature and seasonal phenology may be too rapid for many species to respond to (Diffenbaugh & Field, 2013). Species' adaptability is further challenged by the difficulty in responding to concurrent, multifarious, and interconnected changes (Diffenbaugh & Field, 2013; Polazzo *et al.*, 2024). In the future, landscapes may thus become unable to support species and population sizes they supported historically, and species may begin selecting against historical ranges (Williams & Blois, 2018). Therefore, it is crucial for conservationists to distinguish between a species' ideal environmental space and its best available geographic space (*sensu* Matthiopoulos, 2022). Accelerating multifarious change in species' movement behaviour and energetic costs require conservation measures that are proactive and anticipate future changes. Polazzo *et al.* (2024) present a framework for estimating species' responses to multifarious change using GAMs that is particularly useful when estimating species' (nonlinear) responses to interactions between environmental variables (e.g., changes in both temperature and limiting nutrients). By accounting for the effects of multiple variables at once, they demonstrate how a species' response to one variable can depend on other concurrent changes. Estimating responses to multifarious change is crucial in assessing mammals' responses to hotter temperatures, altered phenology, and novel community dynamics. Protected areas must support populations not only in present conditions but also as species' needs and behaviour change over the decades (Simmons *et al.*, 2021; Livingstone *et al.*, 2023). Recent evidence has questioned whether current protected areas will be effective in the long term (Loarie *et al.*, 2009; Diffenbaugh & Field, 2013; Williams & Blois, 2018), and increasingly more experts have been calling for proactive and long-term conservation. By identifying and actively protecting climate change refugia and corridors, we may be able to reduce the effects of climate change on mammalian movement behaviour and community-level responses and ensure that protected areas may be viable for decades to come (Michalak *et al.*, 2018;

<sup>499</sup> Graham *et al.*, 2019; Stralberg *et al.*, 2020; Hua *et al.*, 2022).

<sup>500</sup> Future work should develop models that account for covariates that are specific to the  
<sup>501</sup> study species and area, such as forest age and disturbance (DeMars *et al.*, 2023), terrain  
<sup>502</sup> ruggedness (White & Gregovich, 2017), anthropogenic linear features (Dickie *et al.*, 2017),  
<sup>503</sup> and growing human presence in wild spaces (Sih *et al.*, 2011; Rice, 2022), including the  
<sup>504</sup> growing risk of human-wildlife conflict (Abrahms *et al.*, 2023; Weststrate *et al.*, 2024). In  
<sup>505</sup> particular, forests in western Canada are highly dynamic over time (Zhang *et al.*, 2015), and  
<sup>506</sup> fires size and burn severity have increased in western Canada in recent decades (Parisien *et*  
<sup>507</sup> *al.*, 2023; Zurowski, 2023). Thus, while our use of a static raster of forest cover allowed for  
<sup>508</sup> simpler models and climate change projections, future studies should account for mammals'  
<sup>509</sup> responses to temporal forest dynamics, including the impacts of fire (Parisien *et al.*, 2023;  
<sup>510</sup> Zurowski, 2023), logging (Lochhead *et al.*, 2022) and other extractive industries (Dickie *et*  
<sup>511</sup> *al.*, 2017, 2024). However, the inclusion of temporally dynamic variables will require that  
<sup>512</sup> any future projections of species' behaviour depend on temporally dynamic estimates of how  
<sup>513</sup> such variables will change over time with changes in climate and anthropogenic activity.

<sup>514</sup> We have demonstrated that temperature has complex and nonlinear effects on how and  
<sup>515</sup> where mammals move. Rising temperatures have impacted mammals' daily and seasonal  
<sup>516</sup> movement phenology, and changes are expected to intensify throughout the 21<sup>st</sup> century.  
<sup>517</sup> Quantifying how temperature affects mammalian behavior and fitness is a first step towards  
<sup>518</sup> developing an understanding of the effects of climate change on landscape dynamics and the  
<sup>519</sup> effectiveness of protected areas in the future. By leveraging the flexibility and statistical  
<sup>520</sup> power of Hierarchical Generalized Additive Models, we have provided researchers with malleable  
<sup>521</sup> and data-driven methods for assessing species' responses to climate change. We hope  
<sup>522</sup> that future work will develop more species-specific models with the intent of developing a  
<sup>523</sup> community-level framework for quantifying and predicting how communities will respond to  
<sup>524</sup> climate change.

525 **Author contributions**

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

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