

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

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## Abstract

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

<sup>1</sup> **1 other refs**

- <sup>2</sup> • Gerlich *et al.* (2025): effects of temperature on fly movement in the arctic
- <sup>3</sup> • “Potential changes in climate indices in Alberta under projected global warming of
- <sup>4</sup> 1.5–5 °C” (<https://www.sciencedirect.com/science/article/pii/S2214581823000770#fig0015>)
- <sup>5</sup> • Global vulnerability of marine mammals to global warming: <https://doi.org/10.1038/s41598-019-57280-3>
- <sup>6</sup> • marine turtles shift and lose habitat with temperature: <https://www.science.org/doi/10.1126/sciadv.adw4495>
- <sup>7</sup> • changes in temperature change phenology and movement behaviour as a consequence
- <sup>8</sup> Gerlich *et al.* (2025)
- <sup>9</sup> • Walker *et al.* (2019): Global climate change and invariable photoperiods: {A} mismatch that jeopardizes animal fitness
- <sup>10</sup>
- <sup>11</sup>
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- <sup>13</sup>

<sup>14</sup> **2 Introduction**

<sup>15</sup> For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan  
<sup>16</sup> *et al.*, 2008). Animals move to optimize resource use (e.g., food, water, shelter; Charnov,  
<sup>17</sup> 1976; Kacelnik *et al.*, 1992; Merkle *et al.*, 2016; Mezzini *et al.*, 2025), optimize habitat use  
<sup>18</sup> (Schwerdt *et al.*, 2024; Winter *et al.*, 2024), and avoid predators and competitors (Tórrez-  
<sup>19</sup> Herrera *et al.*, 2020; Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024).  
<sup>20</sup> However, ambient temperature affects mammals' movement rates by altering the energetic  
<sup>21</sup> cost of movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016;  
<sup>22</sup> Jahn & Seebacher, 2022) and the risk of hyperthermia (Hetem *et al.*, 2014; Dyer *et al.*, 2023).  
<sup>23</sup> Animals may search for a short-term buffer from extreme heat or cold via thermal refugia  
<sup>24</sup> (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;  
<sup>25</sup> Gulland *et al.*, 2022), which may even be preferred over forage abundance (Hall *et al.*, 2016).  
<sup>26</sup> By altering mammals' movement speed and habitat use (jointly, their movement behaviour:  
<sup>27</sup> Nathan *et al.*, 2008, 2022), ambient temperature also affects the consequences of movement  
<sup>28</sup> behaviour (Alston *et al.*, 2020; Giroux *et al.*, 2023), such as encounter rates with resources  
<sup>29</sup> (Mezzini *et al.*, 2025), humans (Weststrate *et al.*, 2024), predators, prey, or competitors  
<sup>30</sup> (Martinez-Garcia *et al.*, 2020; Glass *et al.*, 2021; Brivio *et al.*, 2024). Behavioural changes  
<sup>31</sup> to temperature are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018)  
<sup>32</sup> and extreme heat (Powers *et al.*, 2017; Alston *et al.*, 2020; Giroux *et al.*, 2023; Verzuh *et al.*,  
<sup>33</sup> 2023).

<sup>34</sup> Mammals are particularly susceptible to adverse effects from excessive heat (Sherwood &  
<sup>35</sup> Huber, 2010). While extreme cold often leads to reduced movement, provided that individ-  
<sup>36</sup> uals can find refuge and take advantage of their body heat (Berger *et al.*, 2018; Hou *et al.*,  
<sup>37</sup> 2020; Glass *et al.*, 2021), extreme heat can often result in more severe physiological damage  
<sup>38</sup> in a shorter span of time (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021;  
<sup>39</sup> Newediuk *et al.*, 2024). Due to mammals' difficulty at dissipating heat, particularly when

40 ambient temperatures are near or above their body temperature, they are particularly sen-  
41 sitive to extreme heat, especially with increasing body size (Dyer *et al.*, 2023; Verzuh *et al.*,  
42 2023). Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature  
43 specialists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tri-*  
44 *dactyla*: Giroux *et al.*, 2023), while species that experience wide ranges of temperature vari-  
45 ation (i.e., ‘temperature generalists’) can adapt more easily to change (Levins, 1974; Botero  
46 *et al.*, 2015; Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they  
47 are subject to changes that are more severe (McCain, 2019; Rantanen *et al.*, 2022), affect  
48 many factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource  
49 availability: Polazzo *et al.*, 2024), or are too rapid and severe to respond within a lifetime  
50 or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

51 In the last century, many ecosystems experienced widespread warming that resulted in  
52 milder and shorter winters, hotter and longer summers, and a greater risk of extremely high  
53 temperatures (IPCC, 2023). As heat stress intensifies over the next 100 years, mammals will  
54 continue to suffer impacts on their fitness, movement rates, and habitat selection (Deb *et*  
55 *al.*, 2020; Woo-Durand *et al.*, 2020), which will be exacerbated by more frequent and intense  
56 extreme events (Bunnell *et al.*, 2011) and anthropogenic habitat loss, modification, and frag-  
57 mentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). It remains unclear  
58 how or whether species will be able to respond to climate change in the current century (Deb  
59 *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially if populations fail to  
60 adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable  
61 to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Preparing for and responding  
62 to future changes require a comprehensive understanding of how temperature will affect how  
63 and where mammals move, as well as the implications such changes will have on species’  
64 adaptability and overall community structure. Recent work has documented the effects of  
65 climate change on mammals’ ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*,  
66 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size,

67 activity time, and elevational and latitudinal distribution McCain, 2019). However, there  
68 remains a need for fine-scale estimates of the effects of temperature on mammals' movement  
69 behaviour and quantitative predictions of how their behaviour will respond to climate change  
70 in the current century (IPCC, 2023).

71 Western Canada is currently experiencing rapid widespread warming (Turner & Clifton,  
72 2009; Kienzle, 2018; Dierauer *et al.*, 2021), phenological shifts (Kienzle, 2018; Basu *et al.*,  
73 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et al.*, 2023),  
74 including forest fires (Zurowski, 2023). As we approach the deadline for the Kunming-  
75 Montreal Global Biodiversity Framework (i.e., the “30 by 30” initiative), a global effort to  
76 conserve 30% of the world’s lands and oceans by 2030 (Convention on Biological Diversity,  
77 2022), Canadian decision makers must understand which areas will be of greatest value for  
78 maximizing and protecting biodiversity not only for current conditions but future decades,  
79 too. Failing to understand how climate change will affect mammalian movement behaviour  
80 will hinder our ability to respond to the current climate crisis and make decisions that are  
81 viable in the long term. Furthermore, understanding how temperature affects individual  
82 species is the first step towards understanding how temperature impacts the community  
83 dynamics (Hegel *et al.*, 2010) and habitat phenology (Bunnell *et al.*, 2011; Duncan *et al.*,  
84 2012; Merkle *et al.*, 2016; Slatyer *et al.*, 2022).

85 In this paper, we quantify the effects of proximal air temperature on mammalian move-  
86 ment behaviour, namely movement rates and habitat selection of six large-bodied terrestrial  
87 mammal species in western Canada (wolves: *Canis lupus*, elk: *Cervus canadensis*, moun-  
88 tain goats: *Oreamnos americanus*, cougars: *Puma concolor*, boreal and southern mountain  
89 caribou: *Rangifer tarandus*, and grizzly bears: *Ursus arctos horribilis*; Table 1). Using over  
90 25 years of telemetry data throughout a large spatial range of western Canada and hourly  
91 air temperature data, we estimate how these mammals altered their probability of mov-  
92 ing, speed when moving, and habitat selection in response to temperature. We then pair  
93 the estimated responses with climate change projections to forecast the species’ movement

94 behaviour during the 21<sup>st</sup> century under different climate-change scenarios (referred to as  
 95 Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss the consequences of  
 96 these changes in movement behaviour at the individual, population, and community levels.  
 97 We also provide directions for future research and solutions for overcoming some common  
 98 data limitations.

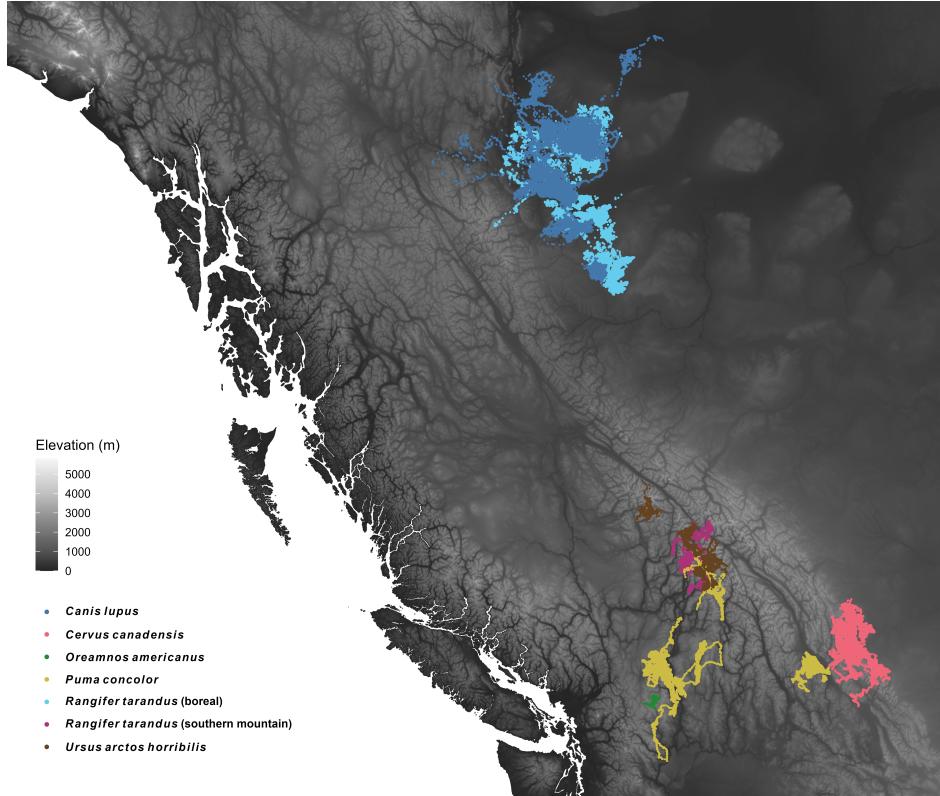


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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

| Species                                | Start      | End        | $\Delta t$ (hours) | Animals | Has speed |
|--|------------|------------|--------------------|---------|-----------|
| <i>Canis lupus</i>                     | 2013-01-27 | 2017-08-29 | 0.25               | 39      | 39        |
| <i>Cervus canadensis</i>               | 2007-01-13 | 2013-11-20 | 2.00               | 169     | 169       |
| <i>Oreamnos americanus</i>             | 2019-06-25 | 2023-10-05 | 6.25               | 11      | 10        |
| <i>Puma concolor</i>                   | 2006-02-05 | 2021-07-13 | 2.00               | 29      | 29        |
| <i>Rangifer tarandus</i> (boreal)      | 2011-03-02 | 2018-01-04 | 13.00              | 146     | 131       |
| <i>Rangifer tarandus</i> (s. mountain) | 1998-03-21 | 2009-06-07 | 6.00               | 22      | 20        |

| Species                        | Start      | End        | $\Delta t$ (hours) | Animals | Has speed |
|--------------------------------|------------|------------|--------------------|---------|-----------|
| <i>Ursus arctos horribilis</i> | 2004-09-30 | 2009-09-07 | 1.00               | 18      | 18        |

### 99 3 Methods

100 3.1 Datasets used

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

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

110 3.1.1 GPS telemetry data

111 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
 112 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022). Boreal caribou (*Rangifer*  
 113 *tarandus*) and wolf (*Canis lupus*) telemtries were acquired from a data repository of the  
 114 British Columbia Oil and Gas Research and Innovation Society (BC OGRIS) that was col-  
 115 lected as part of the boreal caribou radio-collaring program of the BC OGRIS Research  
 116 and Effectiveness Monitoring Board (REMB; BC OGRIS, 2018). **MISSING INFO ON**  
 117 **OTHER TELEMETRY DATA.** From the full set of telemetry data, we removed a total  
 118 of 2396 problematic GPS locations (0.16%, including collar calibration data) after inspect-  
 119 ing diagnostic plots of (1) distance from the median location, (2) straight-line displacement  
 120 between locations, (3) turning angle, and (4) time interval between consecutive points. Par-

121 ticular attention was paid to points with large turning angles ( $\gtrsim 170^\circ$ ) and excessively high  
122 straight-line displacement, especially if antecedent and subsequent points indicated relatively  
123 stationary behaviour (Appendix A).

### 124 3.1.2 Historical temperature data and climate change projections

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

131 We used the the `climatenetR` package (v. 1.0, Burnett, 2023) for `R` and `ClimateNA` (v.  
132 7.4.2; Wang *et al.*, 2016; Mahony *et al.*, 2022) to obtain projected average monthly temper-  
133 atures from 2020 to 2100 at a  $0.08^\circ$  spatial resolution. Since the climate projections only  
134 provided monthly means and ranges but no measures of variance or distributional assump-  
135 tions, we used the historical data for western Canada from 1998 to 2023 (extremes included)  
136 to estimate the monthly variation in temperature, which we defined as  $\sigma_T^2$ , the variance at  
137 location  $\langle x, y \rangle$  in month  $m$  for each year (e.g., the variance at coordinates  $\langle -119.40, 49.94 \rangle$   
138 in April 2005). We then modeled the estimated variance using a Generalized Additive Model  
139 for Location and Scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007;  
140 section 7.9 in Wood, 2017) using the `mgcv` package for `R` (v. 1.9-1, Wood, 2017). The linear  
141 predictor for the location (i.e., the mean) included smooth terms of: each year's estimated  
142 within-pixel monthly mean temperature ( $\hat{\mu}_T$ ), month ( $m$ ), a two-dimensional smooth of spa-  
143 tial coordinates  $\langle x, y \rangle$ , and a tensor product interaction term of month and space to allow  
144 for seasonal terms to vary smoothly over space. The linear predictor for the scale term,  
145 which governs the mean-variance relationship (table 3.1 on p. 104 of Wood, 2017), included  
146 smooth terms of the monthly mean temperature, month, and space. We did not include

<sup>147</sup> smooth terms of year to avoid unrealistic projections when extrapolating beyond 2023.

<sup>148</sup> The model was thus

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

<sup>149</sup> where  $\mu_{\sigma_T^2}$  and  $\nu_{\sigma_T^2}$  indicate the location and scale parameters of the gamma distribution of  
<sup>150</sup>  $\sigma_T^2$ , and together they determine the variance of  $\sigma_T^2$ , indicated as  $\mathbb{V}(\sigma_T^2)$ . Functions  $f_{L,j}$  and  
<sup>151</sup>  $f_{S,j}$  indicate the  $j^{\text{th}}$  smooth functions for the location and scale parameters, respectively.

<sup>152</sup> To ensure the smooth functions of month,  $f_{L,2}(m)$  and  $f_{S,2}(m)$ , joined smoothly between  
<sup>153</sup> December and January, the terms use cyclic cubic spline bases. The spatial terms used two-  
<sup>154</sup> dimensional Duchon splines, a generalization of thin-plate regression splines (p. 221 of Wood  
<sup>155</sup> (2017)). The smoothness parameters were estimated via REstricted Maximum Likelihood  
<sup>156</sup> (REML; p. 83 of Wood, 2017). See the Data Availability Statement for additional information  
<sup>157</sup> on the code used to fit the model.

<sup>158</sup> We simulated hourly variation in future years by assuming hourly temperature followed  
<sup>159</sup> a normal distribution with mean specified by the monthly `climatenar` climate projections  
<sup>160</sup> and variance as specified by the gamma GMLS. For each month within each year from  
<sup>161</sup> 2025 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the  
<sup>162</sup> 0.9 quantiles by increments of 0.1, and we weighted each quantile proportionally to the  
<sup>163</sup> (normalized) Gaussian probability density for each quantile.

164 **3.1.3 Resource rasters**

165 We estimated percent forest cover and distance from water using the rasters created by  
166 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
167 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
168 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
169 raster of percent cover of open water (class 12) to a binary raster of pixels with water  
170 (cover > 0%) or without water (cover = 0%) and then calculated each pixel's distance  
171 from the nearest pixel with water using the `distance()` function from the `terra` package.  
172 Finally, we obtained two digital elevation models using the `get_elev_raster()` function  
173 from the `elevatr` package (v. 0.99.0, Hollister *et al.*, 2023). We used a raster with a zoom  
174 of 6 (a resolution of 0.009°) for model fitting and one with a zoom of 3 (a resolution of  
175 0.08°) for downloading climate change projections via `climatenar`. All final rasters and  
176 code are available in the GitHub repository associated with this manuscript (see the Data  
177 Availability Statement).

178 **3.2 Estimating mammals' instantaneous speeds**

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

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

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

195 **3.3 Estimating the effects of temperature on mammals' movement behaviour**

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

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

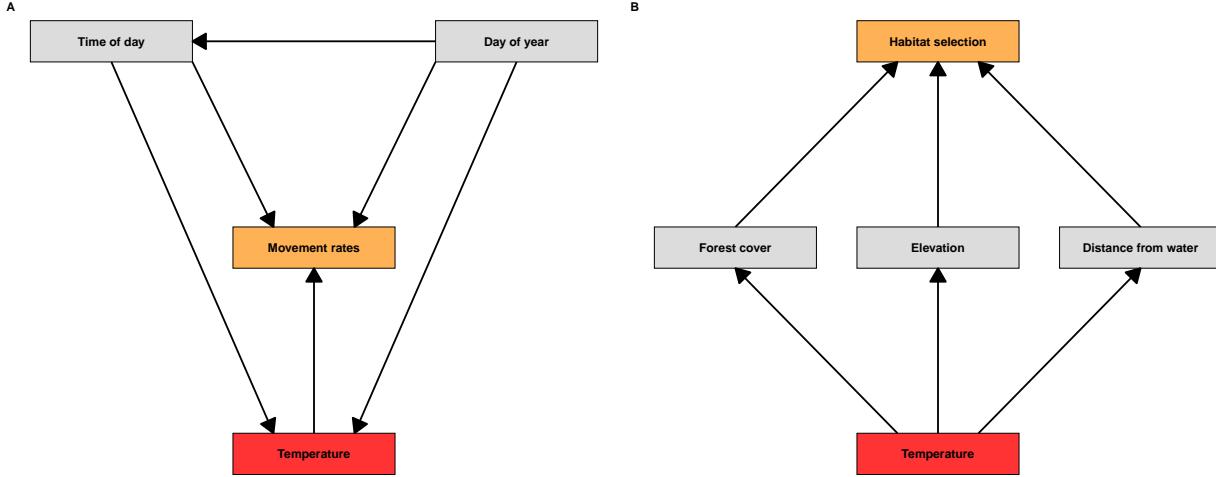


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature on each species' movement behaviour. (A) Ambient temperature affects mammals' movement rates (i.e. probability of moving, speed when moving, and distance traveled), but temperature is influenced by time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

### 214 3.3.1 Effects of temperature on movement rates

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

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

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

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

245 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>246</sup> In both models,  $\beta_s$  indicates a fixed intercept for species  $s$ ,  $Z_a$  indicates a Gaussian random  
<sup>247</sup> effect for animal  $a$  (of species  $s$ ),  $f_{j,s}$  indicates the  $j^{\text{th}}$  smooth function for species  $s$ , and  
<sup>248</sup> functions with two variables indicate tensor product interaction terms. The model code used  
<sup>249</sup> to fit the models is available in Appendix B.

<sup>250</sup> **3.3.2 Effects of temperature on habitat selection**

<sup>251</sup> We estimated the effects of temperature on each species' selection for percent forest cover  
<sup>252</sup> (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
<sup>253</sup> ting a Hierarchical Resource Selection Function (HRSF) for each species. We fit each HRSF  
<sup>254</sup> using an HGAM with a Poisson family of distributions and log link function (Appendix B;  
<sup>255</sup> Aarts *et al.*, 2008). After removing non-resident individuals (Table B1), we accounted for the  
<sup>256</sup> spatiotemporal autocorrelation in the telemetry locations by weighting each point based on  
<sup>257</sup> the telemetry's Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noo-  
<sup>258</sup> nan *et al.*, 2019b; Alston *et al.*, 2022) to produce estimates of second-order habitat selection  
<sup>259</sup> (Johnson, 1980). Quadrature points were determined using the raster cells in each animal's  
<sup>260</sup> 99.9% AKDE percentile and given a weight of 1. The number of quadrature locations greatly  
<sup>261</sup> outnumbered the number of observed locations (Fig. B12), especially after accounting for  
<sup>262</sup> the AKDE weights (Fig. B13).

263 Each species' model had the same structure:

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

264 where the species-level indices are omitted for readability, but each term in the model can  
265 be assumed to be species-specific. Smooth effects of percent forest cover (`forest_perc`),  
266 elevation (`elev_m`), and distance to water (`dist_water_m`) accounted for the species-level  
267 selection strength for each resource. A Gaussian random effect for each individual animal  
268 ( $Z_a$ ) corrected for uneven sampling across individuals, while factor-smooth interaction terms  
269 for each animal ( $f_{j,a}$ ) accounted for animal-level resource selection (i.e., individual-level  
270 deviations from the species-level estimate; Jeltsch *et al.*, 2025). Tensor product interaction  
271 terms of the three resources and temperature (`temp_c`) estimated the smooth change in  
272 resource selection at different temperatures. Finally, marginal smooth terms of temperature  
273 and factor-smooth interaction terms of temperature and animal accounted for species- and  
274 individual-level sampling biases at different temperatures (e.g., sampling more during warm  
275 periods).

## 276 4 Results

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

280 B8). Consequently, we present all results while predicting specifically for one-hour sam-  
 281 pling intervals. At 0°C, species differed in mean probabilities of moving ( $\hat{P}(M)$ ; range:  
 282 0.05 – 0.31), mean speed when moving ( $\hat{\mathbb{E}}(S|M = 1)$ ; range: 0.42 – 2.67 km/h), and mean  
 283 distance traveled (i.e.,  $\hat{P}(M) \times \hat{\mathbb{E}}(S|M = 1)$ , range: 0.04 – 0.61 km/h; Table 2). Griz-  
 284 zly bears had the lowest movement frequency ( $\hat{P}(M) \approx 0.05$ ), while wolves and cougars  
 285 moved most often ( $\hat{P}(M) \geq 0.22$ ). Mountain goats and southern mountain caribou moved  
 286 the slowest ( $\hat{\mathbb{E}}(S|M = 1) \approx 0.43$  km/h), while wolves had the highest mean speed when  
 287 moving ( $\hat{\mathbb{E}}(S|M = 1) \approx 2.67$  km/h). Consequently, at 0°C, wolves traveled an average of  
 288  $0.22 \times 2.67$  km/h  $\approx 0.6$  km/h; 2.5 to 16.7 times further than other species.

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

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

289 Near 0°C, wolves selected for dense forest cover ( $\gtrapprox 50\%$ ), elevations near 1 km, and  
 290 distances from water  $< 10$  km; elk selected for forest cover near 50%, elevations between  
 291 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse ( $<$   
 292 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover,  
 293 an elevation of  $\sim 1$  km, and distances from water  $< 10$  km; boreal caribou selected for  
 294 intermediate to dense forest cover, elevations near 500 m, and distances from water  $< 10$

295 km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and  
296 distances from water < 5 km; and grizzly bears selected for sparse forest cover (25-50%),  
297 elevation near 1 km, and distances from water < 2 km.

298 There was relatively strong agreement between models with and without temperature  
299 (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses  
300 of deviance showed that temperature significantly affected movement behaviour (all p-values  
301  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \geq 342$ ; Table B2 and following pages in Appendix B). Accounting  
302 for temperature resulted in a simpler HRSF for mountain goats (lower model degrees of  
303 freedom) that fit the data better (lower deviance), and hence no test was necessary to show  
304 that the inclusion of temperature produced a better fit.

305 **4.1 Effects of temperature on movement rates**

306 The effects of temperature on movement rates varied in both direction and magnitude across  
307 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
308 migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and  
309 indicated clear shifts in activity over time of day and day of year for all species. The models  
310 had good in-sample prediction (Fig. B7) and explained reasonably high proportions of the  
311 deviance (79.3% for the gamma model and 10.7% for the binomial model, which is relatively  
312 high for a binomial model with binary responses: see ch. 11 of McElreath (2020)]. All  
313 species adapted their daily and seasonal movement behaviour to changes in temperature  
314 (Fig. 3). The clearest example of this was cougars. In mid summer, they moved mostly  
315 in the evening if temperatures were cool and mostly in the early morning if temperatures  
316 were hot. Throughout the year, they tended to move more when it was colder, but what  
317 they perceived as “colder” depended on the time of year. However, uncertainties around  
318 the estimated effects were often higher at extreme temperatures due to data scarcity. All  
319 species’ estimated probability of moving decreased with sampling intervals approximately  
320 above 1 hour, and most species’ estimated speed when moving decreased monotonically with

321 sampling interval, although the estimated trends were highly uncertain for some species (Fig.  
 322 B8).

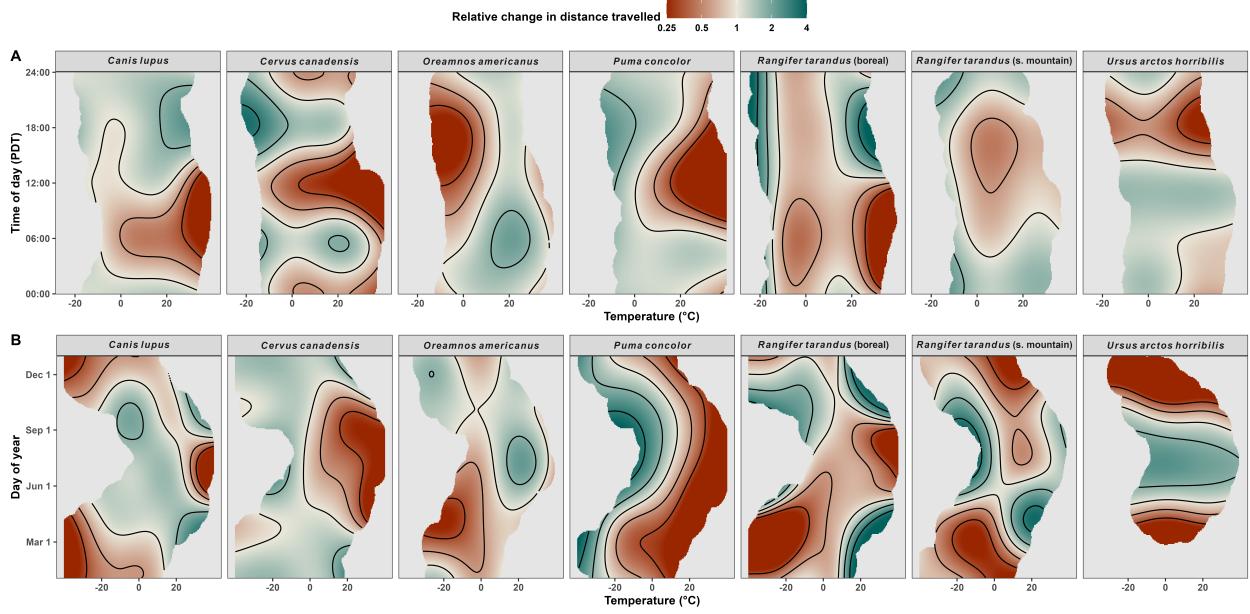
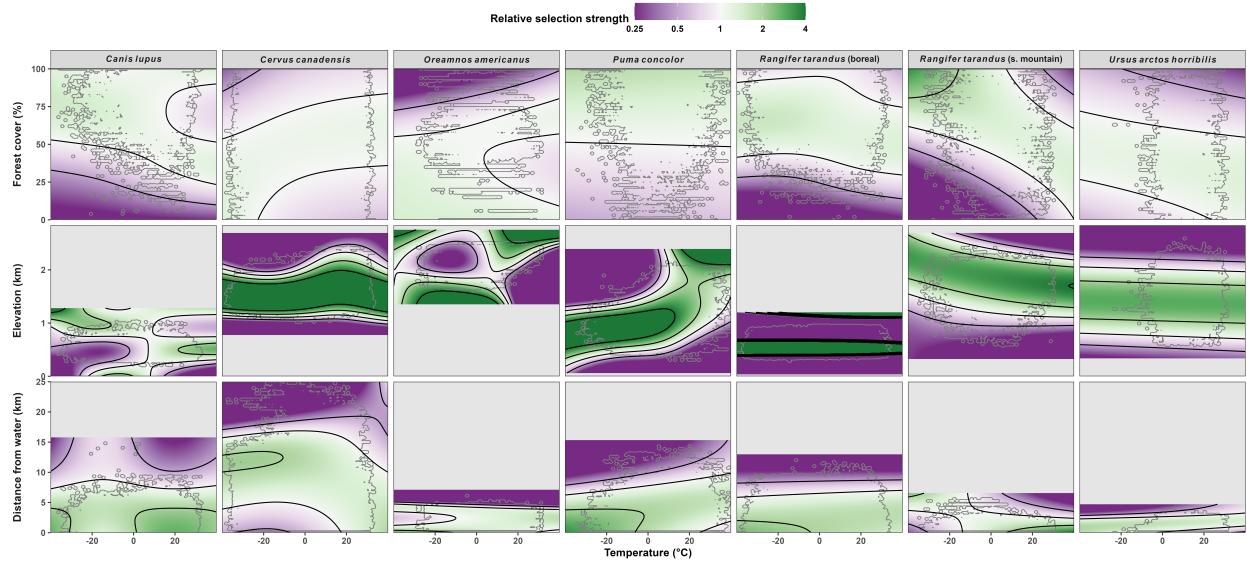


Figure 3: **Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year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

## 323 4.2 Effects of temperature on habitat selection

324 Species' relative selection strength (RSS) was generally strongest for elevation and weak-  
 325 est for forest cover, but species' RSS for resources depended on temperature (Fig. 4).  
 326 Changes in RSS with temperature were also strongest for elevation and generally weak-  
 327 est distance from water, but there were no common trends across all species for any of the  
 328 three resources. All species, with the exception of cougars, exhibited a clear temperature-  
 329 dependent shift in their preference for forest cover. At higher temperatures, wolves, mountain  
 330 goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted  
 331 towards more intermediate forest cover without much of a change in preference width. All  
 332 species shifted elevationally with temperature, although boreal caribou's selection strength  
 333 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain  
 334 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,

and grizzly bears decreased in elevation. Most species generally remained within 5 km of water, and temperature did not affect their selection strength as much as for the other two resources. Again, estimated RSS values were generally most uncertain at extreme temperatures (Fig. B15).



**Figure 4: Temperature strongly affects mammals' habitat selection.** 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.

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

The predicted changes in distance traveled varied across species in both direction and magnitude, but worse climate-change SSPs always corresponded to greater absolute changes (Fig. 5). Additionally, species that were predicted to move less often did not necessarily have lower speeds when moving, and vice versa (Figs. B9 and B10). Overall, absolute changes by 2100 under the best-case SSP were small (approximately 0% to +4%), while under the worst-case SSP absolute changes ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while the models estimated that grizzly bears would move substantially less (if at all) in winter (Figs. 3, B4-B6), the models did not explicitly account for changes in hibernation phenology. Consequently, the climate change projections do not explicitly account for changes in energetic needs or physiology. Projected changes also varied spatially due to heterogeneity in projected climate change (Fig. 6). Again, absolute changes were generally greatest under

351 worse SSPs, but the direction of change at each location also varied across SSPs (most visible  
 352 in cougars).

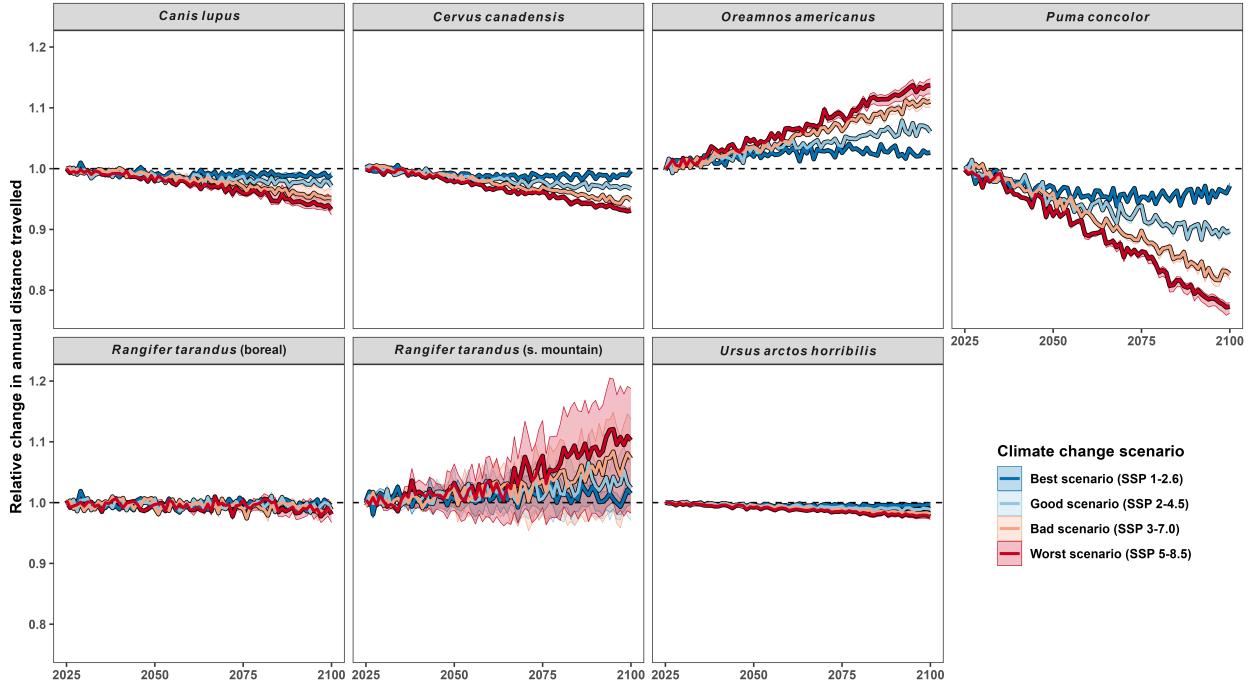
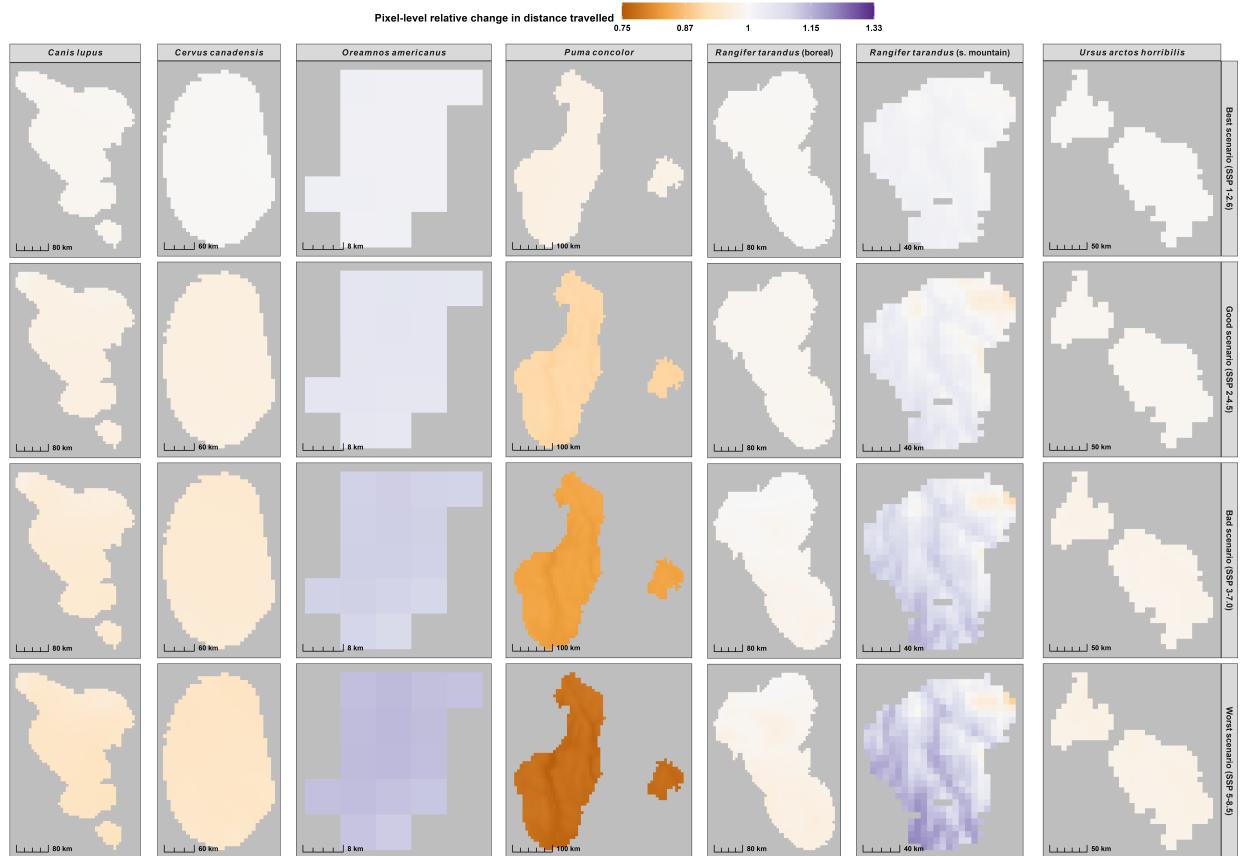


Figure 5: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within each species' observed extent. Shaded areas indicate the range of predicted values between the 95<sup>th</sup> and 5<sup>th</sup> percentiles. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). If the intervals are fully above the dashed line, at least 90% of the estimated means increased, relative to the each pixel's average of the four climate SSPs in 2025. Similar conclusions can be drawn regarding a decrease if the ribbons are below the dashed line. The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

353 Median RSS was projected to decrease over time within the each species' observed range,  
 354 but changes were stronger under worse SSPs (Fig. 8). Decreases were most pronounced in  
 355 the bottom fifth percentile and most severe for elk, southern mountain caribou, and mountain  
 356 goats. Of all the species, only cougars showed a clear increase in RSS for areas within their  
 357 current range. The change in RSS between 2025 and 2100 varied spatially for all species  
 358 (Fig. 8). All species were predicted to exhibit a decrease in RSS throughout most of their  
 359 observed habitats, although cougars were predicted to increase their selection for patches  
 360 with higher altitude.



**Figure 6: Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each pixel's average distance 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 0.67 and 1.5 ( $\approx 2^{0.585}$ ; original data ranged 0.50 to 1.56). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest density. All maps are shown with a BC Albers projection (EPSG:3005).

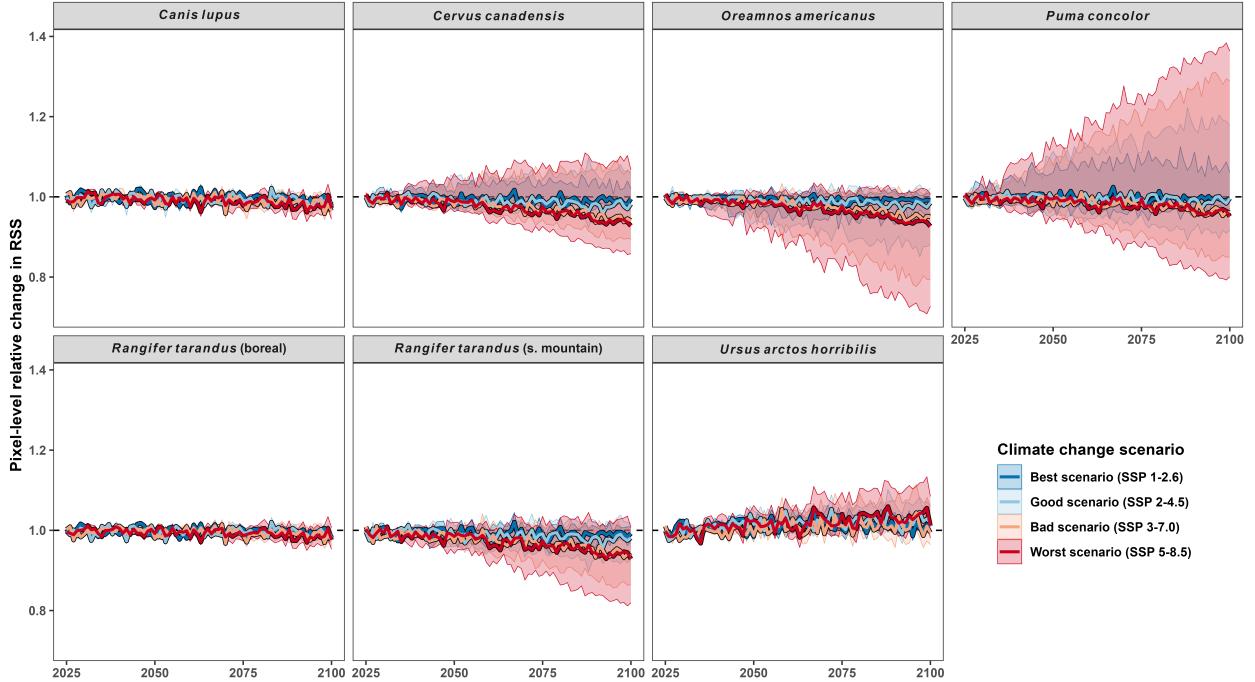
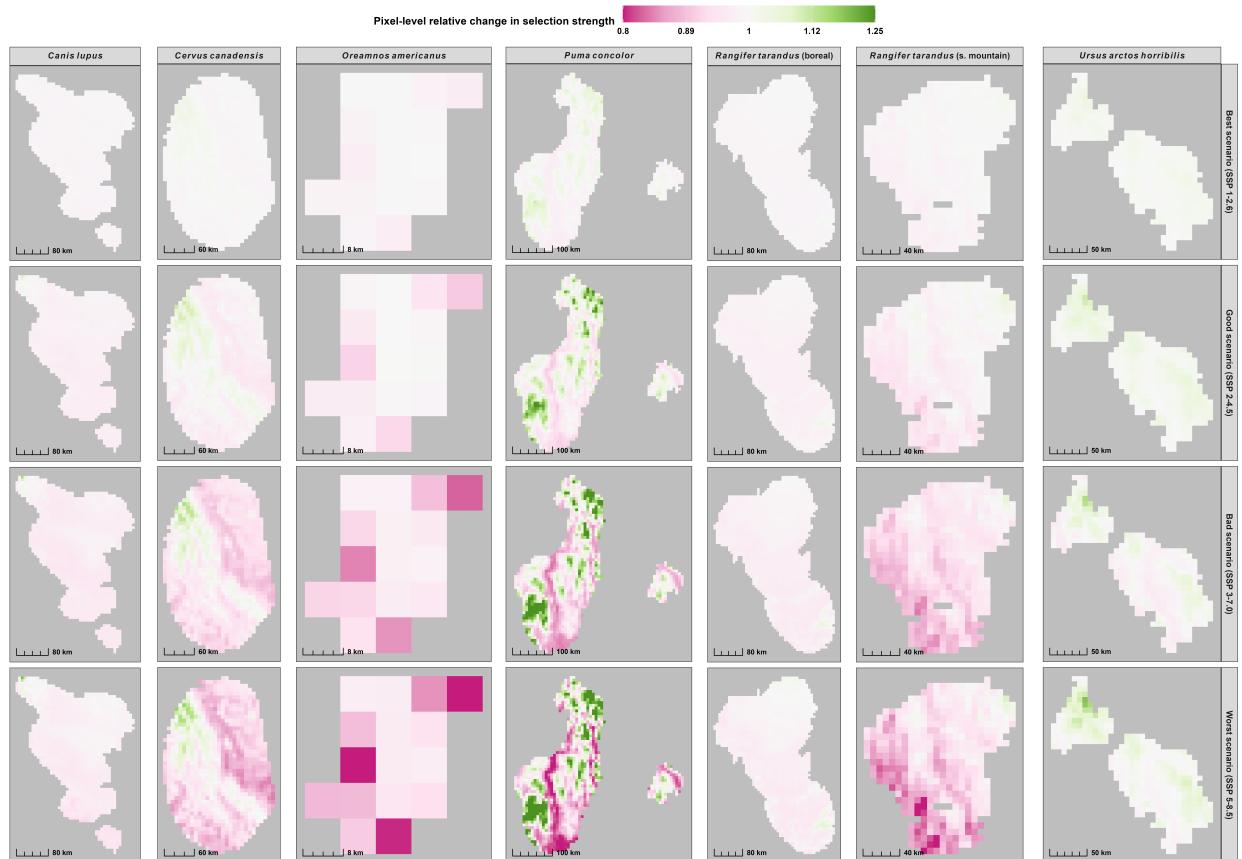


Figure 7: All species are expected to exhibit a decrease in median relative selection strength (RSS) for their current range, irrespective of climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within each species' observed extent within BC, while the ribbons indicate the range between the 95<sup>th</sup> and 5<sup>th</sup> percentiles in RSS. Changes are relative to each location's mean RSS in 2025 across the four Shared Socioeconomic Pathways (SSPs).

## 361 5 Discussion

362 We have demonstrated that temperature is an important determinant of whether, how,  
 363 and where large mammals move, even while accounting for seasonality (e.g., changes in  
 364 photoperiod, hormones, and resources). Disentangling temperature from other drivers is  
 365 important for predicting how changes in climate will affect mammalian movement when  
 366 other drivers remain approximately constant. However, predicting mammals' responses to  
 367 climate change becomes increasingly complex as habitats warm and animals are exposed to  
 368 increasingly frequent conditions that are both extreme and novel.

369 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3  
 370 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.  
 371 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;  
 372 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,  
 373 and/or prey can often be substantially different from the behaviour at typical temperatures.



**Figure 8: Climate change will impact each species' habitat 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 0.67 and 1.5 ( $\approx 2^{\pm 0.585}$ ; original data ranged 0.66 to 1.86). All maps are shown with a BC Albers projection (EPSG:3005).

<sup>374</sup> As extreme temperature events become more frequent and prolonged throughout the year  
<sup>375</sup> (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-  
<sup>376</sup> haviours that may alter community structures and behaviours, both during such events and  
<sup>377</sup> afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,  
<sup>378</sup> changes in climate and phenology impact the life history and behaviour of many hibernat-  
<sup>379</sup> ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality  
<sup>380</sup> (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

<sup>381</sup> Changes in animal movement behaviour may also alter the frequency and intensity of  
<sup>382</sup> human-wildlife conflict, especially with the addition of growing pressures from human de-  
<sup>383</sup> velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At  
<sup>384</sup> the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,  
<sup>385</sup> 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease  
<sup>386</sup> (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being  
<sup>387</sup> preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;  
<sup>388</sup> Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;  
<sup>389</sup> Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences  
<sup>390</sup> for population and ecosystem structures and dynamics as prey, predators, and competitors  
<sup>391</sup> experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*  
<sup>392</sup> *al.*, 2011).

<sup>393</sup> Our ability to respond changes in climate is contingent on our ability to prepare for and  
<sup>394</sup> predict change. However, predicting animal behaviour becomes increasingly complicated as  
<sup>395</sup> the conditions animals are exposed to deviate from current, typical conditions, especially  
<sup>396</sup> when responses are nonlinear and data are sparse. Consequently, we do not present our re-  
<sup>397</sup> sults as a definitive guide to how mammals in western Canada will respond to climate change.  
<sup>398</sup> Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement  
<sup>399</sup> rates and habitat selection depend on temperature and (2) how one can estimate mammals'  
<sup>400</sup> changes in movement behaviour due to climate change. Additionally, communicating un-

certainty in one's estimates is crucial in assessing risk probabilistically, and appropriate measures of uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann, 2014).

*Achieving the “30 by 30” goal will require international collaboration (Huang & Zhai, 2021) as well as active partnership with local Peoples, especially Indigenous Peoples (Wong et al., 2020; Lamb et al., 2023). Understanding the consequences of climate change on mammals’ movement behaviour is a first step towards proactively responding to how mammals will respond to human-induced rapid environmental change (Sih et al., 2011; Williams & Blois, 2018). In the following sections, we discuss the implications of our results in more detail. We then expand on consequences for conservation during the 21<sup>st</sup> century and considerations for future studies.*

## 5.1 Effects of temperature on movement rates

The heterogeneity mammals’ responses to temperature suggests that ecological communities will respond to change in complex and interconnected ways. Although our models do not account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that warmer temperatures cause many species to alter their daily and seasonal activity patterns (most visible in cougars and grizzly bears). For example, when temperatures were above 0°C, cougars moved most at night, but when temperatures were below 0°C they tended to move more throughout the day. Throughout the year, they adapted their tolerance to temperature and moved less when it was relatively hot (for a given time of year), especially in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk, cougars, and boreal caribou when summer temperatures were above 20°C suggests that the increasingly common and intense heat waves across western Canada will have community-wide impacts on movement rates, encounter rates, and potentially community structure (Martinez-Garcia et al., 2020). More work is necessary on quantifying interspecific responses to temperature, including the effects of temperature on predation rates (but see: Cunningham et al., 2021;

<sup>427</sup> Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme  
<sup>428</sup> heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and  
<sup>429</sup> timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,  
<sup>430</sup> 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at  
<sup>431</sup> the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially  
<sup>432</sup> since landscape changes will likely depend not only on the direct effect of temperature but  
<sup>433</sup> also on cascading changes in the availability and unpredictability of resources (McLellan &  
<sup>434</sup> McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

<sup>435</sup> **5.2 Effects of temperature on habitat selection**

<sup>436</sup> As with the effects of temperature on movement rates, the heterogeneity of temperature  
<sup>437</sup> effects on species' habitat selection indicates that efficient and proactive habitat conservation  
<sup>438</sup> will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
<sup>439</sup> physiological responses to temperature that may impact movement, such as changes in the  
<sup>440</sup> phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or  
<sup>441</sup> behaviour (e.g., migration, food caching), other than as direct responses to temperature.  
<sup>442</sup> Consequently, the behavioural changes we present should be interpreted carefully. While  
<sup>443</sup> some seasonal cycles do not depend directly on temperature and may thus not be impacted  
<sup>444</sup> directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the  
<sup>445</sup> predictions we present also rely on the assumption that mammals will not adapt these  
<sup>446</sup> seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage  
<sup>447</sup> availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important  
<sup>448</sup> to stress the distinction between habitat selection and quality. While animals tend to select  
<sup>449</sup> for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can  
<sup>450</sup> also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,  
<sup>451</sup> 2021).

- <sup>452</sup> • geographic space *sensu* Matthiopoulos (2022)

- 453     • environmental space *sensu* Matthiopoulos (2022)
- 454     • G space is the realization of the theoretical E space

455     **5.3 Predicted changes in movement during the 21<sup>st</sup> century**

456       Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on  
457       Biological Diversity, 2022) will require careful planning but often also rapid action. In the  
458       case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the  
459       end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment  
460       and Climate Change, 2024). Additionally, efficient and effective conservation will require  
461       collaboration with Indigenous and local communities to ensure Treaties are respected in the  
462       process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,  
463       2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,  
464       2021).

465       The diversity in predicted changes in movement behaviour by 2100 (both across species  
466       and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the  
467       need for careful planning that incorporates not only reliable estimates of change but also  
468       pragmatic and communicable measures of uncertainty and variability around such estimates.  
469       For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-  
470       individual variation should be accounted for when deciding the location and size of protected  
471       areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly  
472       limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva  
473       *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on  
474       mammals’ movement require a holistic view of the direct effects of temperature on mammals’  
475       movement directly as well as its effects on other drivers of movement, such as forage and prey  
476       availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,  
477       2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,  
478       2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation

among the responses of different species (and individuals), especially as populations undergo a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and likely decreases), some animals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*, 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

#### 5.4 Species-specific considerations

##### 5.4.1 *Canis lupus*

##### 5.4.2 *Cervus canadensis*

##### 5.4.3 *Oreamnos americanus*

##### 5.4.4 *Puma concolor*

attraction for disconnected patches of high elevation could lead to fragmentation or traps

##### 5.4.5 *Rangifer tarandus* (boreal)

Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000 m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and (2) crossing the 500 m to > 1,000 m regions is safe and attractive

##### 5.4.6 *Rangifer tarandus* (s. mountain)

HRSFs do not account for migratory behaviour due to reproduction or predation risk

499 **5.4.7 *Ursus arctos horribilis***

500 **5.5 Considerations for future studies**

501 Our work highlights three central considerations for future research: (1) telemetry sam-  
502 pling rates should be designed primarily in relation to the movement timescales of the species  
503 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of in-  
504 dividuals tracked and the duration of each telemetry should depend not just on population  
505 size but also the rate of environmental change, and (3) predicting changes in movement  
506 behaviour becomes highly complex when responses are nonlinear, especially when changes  
507 depend on many interacting factors (Polazzo *et al.*, 2024) and one is interested in predict-  
508 ing responses in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher,  
509 2020).

510 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,  
511 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-  
512 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.  
513 This dependency is because coarsely-sampled movement data contains information on large-  
514 scale movements (range crossings, migrations) but not fine-scale movements, including first-  
515 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour  
516 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-  
517 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement  
518 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional  
519 examples of how the frequency of location data affects the results that can be inferred by  
520 modeling movement behaviour. Consequently, we suggest being cautious when comparing  
521 estimated movement behaviours across species, even though all predictions have been cor-  
522 rected to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`).  
523 Ideally, sampling schedules should be fine enough to reconstruct animals' movement move-  
524 ment paths. Good estimates of an animal's speed and trajectory require telemetry locations

525 to be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so  
526 that, on average, the dataset contains multiple locations in between changes in direction.  
527 What constitutes a change in direction depends on what movement scale one is investigating.  
528 Small-scale movements and first-order spatial selection will require more frequent sampling  
529 than migratory movement or second-order and third-order spatial selection. While ctmm  
530 movement models are scale-invariant in that any model can be scaled to larger or smaller  
531 areas and timescales, the model estimates are not independent of the scale of the sampling  
532 frequency.

533 When landscapes are relatively predictable across years, a larger number of sampled  
534 individuals is likely preferable over the duration of each tracking period. The greater number  
535 of tracked animals allows one to quantify the variance across individuals, including the  
536 range of conditions and environments that individual animals are in. A good estimate of  
537 inter-individual variance provides better coefficient estimates along with more appropriate  
538 measures of uncertainty. However, when conditions across years are stochastic, multi-year  
539 telemtries allow one to better estimate inter-annual variation without conflating it with  
540 inter-individual differences. Given the widespread, rapid, and accelerating changes across  
541 many habitats (particularly at high elevations and at high latitudes), we suggest researchers  
542 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while  
543 increasing the ranges of temperatures each individual is observed in. Longer observational  
544 periods can also improve the chances of observing different community dynamics, such as  
545 shifts in predator-prey dinamics.

546 Temperature affects many aspects of mammalian physiology and behaviour, including  
547 energetics, sleep, and movement behaviour. Climatic changes during the last two centuries  
548 have exposed many mammals to novel and increasingly extreme environmental conditions  
549 that have led to visible changes that impact not only individuals but also ecological and  
550 human communities. However, quantifying the effects of climate change is often complex,  
551 especially as conditions become increasingly different and extreme events become increas-

552 ingly common. Accurately quantifying the nonlinear effects of temperature on when, how,  
553 and where mammals move requires careful data collection and model design. We have pre-  
554 sented a multi-species analysis of the effects of temperature on mammalian movement rates  
555 and habitat selection in hopes that other researchers can leverage this framework and models  
556 to expand our understanding of how temperature affects the movement behaviour of other  
557 species, including smaller mammals, more elusive species, and non-mammal animals. Un-  
558 derstanding of how temperature affects each species in a community will allow us to begin  
559 making community-level inferences of how temperature will affect intra-specific interactions  
560 from a movement behaviour perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*,  
561 2020). While adopting such a perspective is surely not simple, it would result in more com-  
562 plete estimates of the effects of climate change on community ecology, particularly when  
563 species are exposed to rapid change in many important variables. Future work should ex-  
564 plore the effects of temperature on movement behaviour while accounting for finer-scale and  
565 species specific variables that were not accounted for in this study. Examples of these include  
566 temporally dynamic measures of forest type and age, canopy density, competitive pressures,  
567 forage availability, and predator avoidance, or environmental stochasticity. However, many  
568 of these data not available, so we also suggest that more work be done on quantifying such  
569 measures using spatiotemporally dynamic models and sufficiently fine resolutions.

## 570 6 Author contributions

571 SM performed the data cleaning, ran the analyses, and wrote the majority of the  
572 manuscript. CHF wrote code for estimating instantaneous movement speeds. MJN  
573 conceived of the project idea and supervised SM throughout the project. All other authors  
574 contributed telemetry data and contributed to the interpretation of the results for their  
575 species of interest. All authors contributed to reviewing the manuscript.

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