

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

Stefano Mezzini<sup>1,2</sup>      Chris H. Fleming<sup>3,4</sup>      Siobhan Darlington<sup>1,2</sup>

Adam T. Ford<sup>1,2</sup>      TJ Gooliaff<sup>5</sup>      Karen E. Hodges<sup>1,2</sup>      Kirk Safford<sup>6</sup>

Robert Serrouya<sup>1,2,7</sup>      Michael J. Noonan<sup>1,2,8</sup>

<sup>1</sup> Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

<sup>2</sup> Department of Biology, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

<sup>3</sup> Department of Biology, University of Central Florida, Orlando, Florida 32816, United States.

<sup>4</sup> Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Rd., Front Royal, VA 22630, United States.

<sup>5</sup> British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Penticton, BC, Canada.

<sup>6</sup> British Columbia Ministry of Environment and Parks, Penticton, BC, Canada.

<sup>7</sup> Wildlife Science Centre, Biodiversity Pathways, University of British Columbia Okanagan, Revelstoke, British Columbia, Canada.

<sup>8</sup> Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

**Article type:** Research article

**Words in abstract:** 286

**Words in main text:** 7033

**Figures:** 8

**Tables:** 3

**References:** 142 (updated on 2025-06-11)

**Appendices:** 2

**Key words:** climate change, temperature, mammals, animal movement, movement behavior, habitat selection

## 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 behavior cycles. Consequently, it is still unclear how mammals will adapt their movement behavior 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 behavior and community structure will become crucial for effectively and proactively understanding mammalian movement behavior 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 behavior as a consequence Ger-
- <sup>8</sup> lich *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>
- <sup>12</sup>
- <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 behavior:  
<sup>27</sup> Nathan *et al.*, 2008, 2022), ambient temperature also affects the consequences of movement  
<sup>28</sup> behavior (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). Behavioral changes to  
<sup>31</sup> temperature are exacerbated in extreme cold (Wilson *et al.*, 2001; Berger *et al.*, 2018) and  
<sup>32</sup> 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 rapid and serious physiological  
<sup>38</sup> damage (Jessen, 2001; Sherwood & Huber, 2010; Mota-Rojas *et al.*, 2021; Newediuk *et al.*,  
<sup>39</sup> 2024). Due to mammals' difficulty at dissipating heat, particularly when ambient temper-

40 atures are near or above their body temperature, they are particularly sensitive to extreme  
41 heat, particularly if they have a large body size (Dyer *et al.*, 2023; Verzuh *et al.*, 2023).  
42 Furthermore, species that experience narrow temperature ranges (i.e., ‘temperature special-  
43 ists’) tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga tridactyla*:  
44 Giroux *et al.*, 2023), while species that experience wide ranges of temperature variation (i.e.,  
45 ‘temperature generalists’) can adapt more easily to change (Levins, 1974; Botero *et al.*, 2015;  
46 Dupont *et al.*, 2024). Still, generalists’ greater adaptability is tested when they are subject  
47 to changes that are more severe (McCain, 2019; **rantanen\_arctic\_2022?**), affect many  
48 factors at once (e.g., temperature, snow depth, ecosystem phenology, and resource availabil-  
49 ity: Polazzo *et al.*, 2024), or are too rapid and severe to respond within a lifetime or a few  
50 generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

51 In the last 200 years, 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). Over the next 100 years, these changes are expected to worsen  
54 and continue to impact mammals’ fitness, movement behaviour, and habitat selection as  
55 animals cope with growing heat stress (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020) and more  
56 frequent and intense extreme events (Bunnell *et al.*, 2011), along with growing anthropogenic  
57 habitat loss, modification, and fragmentation (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate  
58 *et al.*, 2024). It remains unclear how or whether species will be able to respond to climate  
59 change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*,  
60 2023), especially if populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et*  
61 *al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams  
62 & Blois, 2018). Preparing for and responding to future changes require a comprehensive  
63 understanding of how temperature will affect how and where mammals move, as well as the  
64 implications such changes will have on species’ adaptability and overall community structure.  
65 Recent work has documented the effects of climate change on mammals’ ranges (Leclerc *et al.*,  
66 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*, 2021),

67 and trait-based responses (e.g., body size, activity time, and elevational and latitudinal  
68 distribution McCain, 2019). However, there remains a need for fine-scale estimates of the  
69 effects of temperature on mammals' movement behavior and quantitative predictions of how  
70 their behavior will change in the current century.

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

94 the species' movement behavior during the 21<sup>st</sup> century under different climate-change sce-  
 95 narios (referred to as Shared Socioeconomic Pathways, SSP, Riahi *et al.*, 2017). We discuss  
 96 the consequences of these changes at the individual, population, and community levels. We  
 97 also provide suggestions for future research, including sampling design to overcome some  
 98 common data limitations.

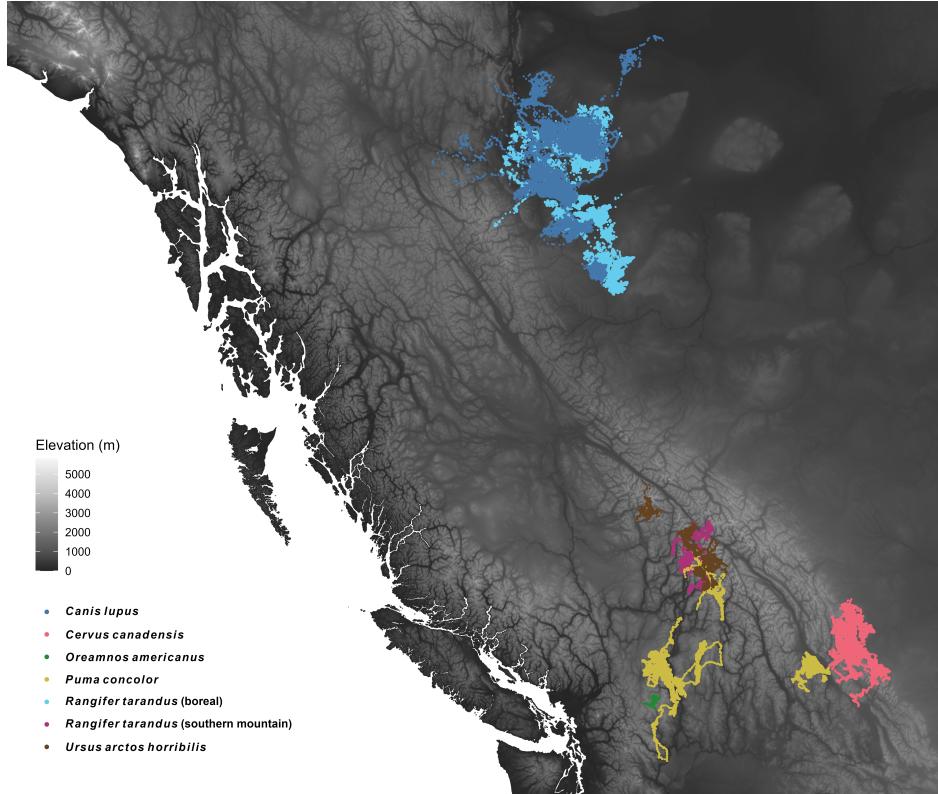


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Start and end of the GPS telemtries along with the median sampling interval ( $\Delta t$ ; stratified by individual), number of animals (Animals), and number of animals with resolved speed (Has speed) for each of the species in this study.

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 reanalyzed air temperature from the ERA5 dataset from  
 103 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent  
 104 forest cover, elevation, and distance from water; and (4) climate change projections under  
 105 four Shared Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). While we acknowledge  
 106 that forest type, structure, and age are important variables, we do not include such variables  
 107 in this study for the sake of parsimony and comparability across species. We detail the data  
 108 sources and analyses in the sections below.

#### 109 3.1.1 GPS telemetry data

110 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
 111 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou  
 112 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public British  
 113 Columbia Oil and Gas Research and Innovation Society repository (<https://www.bcgiris.ca/projects/boreal-caribou-telemetry-data>). **MISSING INFO ON OTHER TELEME-**  
**114 TRY DATA.** From the full set of telemetry data, a total of 2396 GPS locations (0.16%,  
 115 including collar calibration data) were removed using diagnostic plots of (1) distance from  
 116 the median location, (2) straight-line displacement between locations, (3) turning angle, and  
 117 (4) time interval between consecutive points. Particular attention was paid to points with  
 118 large turning angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially if  
 119 antecedent and subsequent points indicated stationary behaviour (Appendix A).

121 **3.1.2 Historical temperature data and temperature projections**

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

128 We obtained rasters of projected monthly average temperature for the study region at a  
129 0.08° spatial resolution from 2020 to 2100 under the different SSPs via the `climatenetR` pack-  
130 age (version 1.0, Burnett, 2023) for R. Since the climate projections only provided monthly  
131 means and ranges but no measures of variance or distributional assumptions, we used the  
132 hourly ERA5 reanalyzed data for western Canada from 1998 to 2023 (extremes included,  
133 Hersbach *et al.*, 2023) to calculate within-month variance in temperature, which we defined as  
134 the variance within a given pixel, month, and year. We then modeled the estimated variance  
135 using a GAM for location and scale (GAMLS, Rigby & Stasinopoulos, 2005; Stasinopoulos &  
136 Rigby, 2007; section 7.9 in Wood, 2017). The linear predictor for the location (i.e., the mean)  
137 included smooth terms of the within-pixel monthly mean temperature (within each year),  
138 month (as a cyclic smooth), a two-dimensional smooth of space, and a tensor interaction  
139 product term of space and month. The linear predictor for the scale term (which governs the  
140 mean-variance relationship) included smooth terms of the monthly mean, month, and space.  
141 We did not include a smooth of year to avoid unrealistic projections when extrapolating  
142 beyond the range of historical data.

143 We simulated hourly variation in future weather by assuming hourly temperature fol-  
144 lowed a normal distribution with mean specified by the monthly `climatenetR` climate pro-  
145 jections and variance as specified by the Gamma GAMLS. For each month within each year  
146 from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to  
147 the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the

148 (normalized) Gaussian probability density for each quantile.

149 **3.1.3 Resource rasters**

150 We estimated percent forest cover and distance from water using the rasters created by  
151 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
152 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
153 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
154 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover  
155 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the  
156 nearest pixel with water using the `distance()` function from the `terra` package. Finally,  
157 we obtained two digital elevation models using the `get_elev_raster()` function from the  
158 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom  
159 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate  
160 change projections via `climatenar`. All final rasters and code are available on GitHub at  
161 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

162 **3.2 Estimating mammals' instantaneous speeds**

163 We modeled each animal's movement using continuous-time movement models (Fleming *et*  
164 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then  
165 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all  
166 models with finite speed estimates (415 of 433, Fleming *et al.*, 2014; Noonan *et al.*, 2019a).  
167 The 18 animals with insufficiently fine sampling to support movement models with finite  
168 speed (Noonan *et al.*, 2019a) were for one mountain goat, 15 boreal caribou, and 2 southern  
169 mountain caribou (Table 1).

170 Since ‘`ctmm`’s movement models assume stochastic but non-zero speeds (i.e., a sin-  
171 gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
172 minimum instantaneous speed could be 0. We performed this correction by subtracting

173 each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
174 used is available on GitHub at [https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend\\_speeds.R](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively  
175 small, non-zero speeds, we determined whether an animal was moving or not using a  $k$ -means  
176 algorithm with 2 clusters for each species' detrended speeds. When the algorithm clearly  
177 failed to discriminate between states, we estimated the split point using the inflection points  
178 in histograms of the detrended speeds (Fig. B1).  
179

### 180 **3.3 Estimating the effects of temperature on mammals' movement**

181 The following sections detail the statistical framework and modelling we used to estimate  
182 the effect on temperature on mammals' movement. To assess the importance of including  
183 temperature as an explicit covariate (rather than including its effects with time of day and  
184 day of year), we fit models with and without smooth effects of temperature and compared  
185 the fits of the two sets of models.

#### 186 **3.3.1 Disentangling direct and indirect effects**

187 In this study, we separate the effects of temperature on mammalian movement into direct  
188 and indirect effects. We call "direct" all effects that impact movement behavior causally  
189 without first impacting another variable (Fig. 2). For example, in Fig. 2A, whether a  
190 grizzly bear is moving in a given moment directly depends on time of day and day of year,  
191 since it will not be moving when sleeping or hibernating. However, time of day and day of  
192 year also impact its movement behavior indirectly because its sensitivity to temperature will  
193 also depend on time of day and day of year. Thus, both time of day and day of year also  
194 impact movement frequency indirectly by altering the effect of temperature on movement  
195 frequency. Failing to disentangle the effects of these three variables will lead to incorrect and  
196 likely confusing estimates for the causal effect of temperature on movement behavior, since  
197 causal and non-causal relationships would be indistinguishable (McElreath, 2020).

198 Indirect effects of temperature also include all effects that can be controlled by altering  
 199 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022). For example, in Fig.  
 200 2B, an increase in temperature may push an animal to prefer higher forest cover in search of  
 201 shade, and conservationists can mitigate these indirect effects of temperature by increasing  
 202 the availability of forested areas, since the effect of temperature on movement is conditional  
 203 on forest cover availability. In contrast, the animal may avoid moving if temperatures are  
 204 above 35°C, irrespective of its geographic and environmental space (*sensu* Matthiopoulos,  
 205 2022). In this case, it is not possible to mitigate the effects of temperature on movement  
 206 behaviour (other than changing temperature directly).

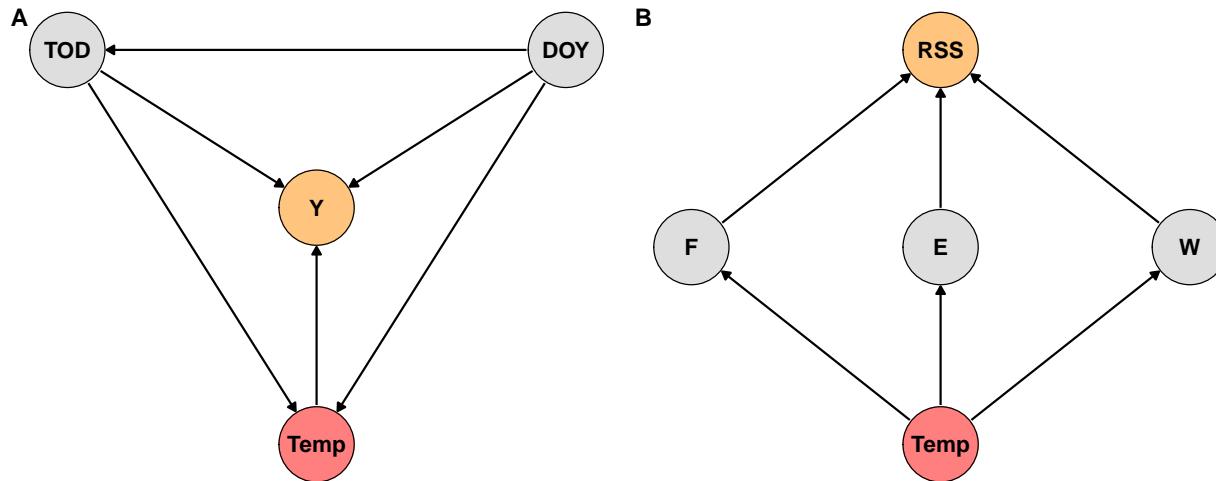


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled (Y) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction effects. Temperature directly affects Y, but the effects of temperature depend on the time of day and season. Time of day and day of year also affect Y directly, but the effect of time of day changes throughout the year due to changes in day length and seasonality. (B) DAG for Relative Selection Strength (RSS) for percent forest cover (F), elevation (E), and distance from water (W). The RSS for of a given habitat depends on all three resources, and the selection for each resource is independent of the other two resources and dependent on temperature.

### 207 3.3.2 Effects of temperature on movement rates

208 We estimated the effects of temperature (°C) on mammals' instantaneous movement state  
 209 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models  
 210 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R  
 211 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was  
 212 moving,  $P(M)$ , with a binomial family of distributions and logit link function. The response

variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an animal's speed when moving (`speed`) with a gamma family of distributions and log link function.

The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`), fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(..., by = species)`), which allowed each species' term to be estimated independent of other species (see 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`). The models also had three tensor product interaction terms (`ti()`) 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: (1) seasonal changes in day length, (2) hourly changes in the response to temperature (e.g., changes in nocturnality), and (3) seasonal changes in the response to temperature (e.g., changes in coats and migration timing). Finally, smooth terms of log-transformed hours between GPS locations (`dt`) accounted for irregular sampling rates. A global term of `log(dt)` accounted for the overall effect of sampling interval, while a factor-smooth interaction term (`s(log(dt), species, bs = 'fs')`) allowed for species-level deviations from the global term while assuming a common smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).

The HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). 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.

```

m_moving <- bam(
  moving ~
    s(animal, bs = 're') +
    species + #' necessary since `by` terms do not include intercept terms
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  data = d,
  method = 'fREML', # fast REML
  discrete = TRUE, # discretize the covariates for faster computation
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5))) #' for `bs = 'cc'` 

m_speed <- bam(
  speed_est ~
    s(animal, bs = 're') +
    species +
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  family = Gamma(link = 'log'),
  data = d_2, #' data filtered for only moving
  method = 'fREML',
  discrete = TRUE,
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5)))

```

### 238 3.3.3 Effects of temperature on habitat selection

239 We estimated the effects of temperature on each species' selection for percent forest cover  
 240 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 241 ting a Hierarchical Resource Selection Function for each species using an HGAM with a  
 242 Poisson family of distributions and log link function (Appendix B; Aarts *et al.*, 2008). After  
 243 removing non-resident individuals (Table B1), we accounted for the spatiotemporal auto-  
 244 correlation in the telemetry locations by weighting each point based on the telemetry's  
 245 Autocorrelated Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b)  
 246 to produce estimates of second- and third-order habitat selection (Johnson, 1980). While  
 247 we recognize there are other important drivers of habitat selection (e.g., forest age, forest  
 248 type, terrain ruggedness, prey availability), we decided to only use these three proxies to  
 249 produce results that are easily comparable across species. Each species' model had the same

250 structure:

```
rsf <- bam(
  detected ~ # 1 for telemetry locations, 0 for quadrature points
  # species-level average resource preference
  s(forest_perc, k = 6, bs = 'tp') +
  s(elevation_m, k = elev_k, bs = 'tp') +
  s(dist_water_m, k = 6, bs = 'tp') +
  # animal-level deviations from the species-level average
  s(animal, bs = 're') +
  s(forest_perc, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(elevation_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  s(dist_water_m, animal, k = 6, bs = 'fs', xt = list(bc = 'cr')) +
  # changes in preference with temperature
  ti(forest_perc, temp_c, k = 6, bs = 'tp') +
  ti(elevation_m, temp_c, k = 6, bs = 'tp') +
  ti(dist_water_m, temp_c, k = 6, bs = 'tp') +
  # include marginals of temperature to remove sampling biases
  s(temp_c, k = 4, bs = 'tp') +
  s(temp_c, animal, k = 4, bs = 'fs', xt = list(bc = 'cr')),
  family = poisson(link = 'log'),
  data = d, # species-specific dataset
  weights = weight, # based on AKDE
  method = 'fREML',
  discrete = TRUE)
```

251 Smooth effects of percent forest cover, elevation, and distance to water accounted for  
252 the species-level average selection strength for each resource. A random effect for each in-  
253 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
254 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
255 selection (i.e., individual-level deviations from the species-level average; Jeltsch *et al.*, 2025).  
256 Tensor interaction product terms (`ti()`) of the three resources and temperature estimated  
257 the change in resource selection at different temperatures. Finally, we included marginal  
258 smooth terms of temperature to account for species- and individual-level sampling biases  
259 over temperature (e.g., sampling more during warm periods). Detections were weighted  
260 proportionally to their degree of independence from other temporally proximate detections  
261 (`weights = weight` – Appendix B; Alston *et al.*, 2022), while quadrature points had a weight  
262 of 1. Quadrature points were obtained using all raster cells in the 99.9% AKDE percentile.  
263 The number of quadrature locations greatly outnumbered the number of observed locations  
264 (Fig. B12), especially after accounting for weighting based on the degree of autocorrelation  
265 and the number of home range crossings (Fig. B13).

266 **4 Results**

267 Overall, 2.6% of GPS locations had temperatures lower than  $-20^{\circ}\text{C}$ , while 6.5% had temper-  
268 atures above  $20^{\circ}\text{C}$ , and temperature ranges differed across species (Table 2, Fig. B2). At  $0^{\circ}\text{C}$ ,  
269 species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed  
270 when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e.,  $P(M) \times \mathbb{E}(S)$ ,  
271 range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ( $P(M) \approx 0.05$ ),  
272 while wolves and cougars moved most often ( $P(M) \geq 0.22$ ). When moving, mountain goats  
273 and southern mountain caribou moved the slowest ( $\mathbb{E}(S|M) \approx 0.43$  km/h), while wolves  
274 had the highest mean speed when moving ( $\mathbb{E}(S|M) \approx 2.64$  km/h). Consequently, wolves  
275 traveled, on average, 0.6 km/h – 2.5 to 16.7 times further than other mammals at  $0^{\circ}\text{C}$ .

Table 2: Percentage of observed GPS locations (after data cleaning) with temperatures below  $-20^{\circ}\text{C}$  or above  $20^{\circ}\text{C}$ .

Species	T < $-20^{\circ}\text{C}$	T > $+20^{\circ}\text{C}$
Canis lupus	1.7 %	13.0 %
Cervus canadensis	2.4 %	4.9 %
Oreamnos americanus	0.7 %	2.8 %
Puma concolor	0.7 %	6.9 %
Rangifer tarandus (boreal)	6.8 %	7.9 %
Rangifer tarandus (s. mountain)	1.3 %	3.4 %
Ursus arctos horribilis	0.0 %	8.4 %
Total	2.6 %	6.5 %

Table 3: Mean probability of movement ( $P(M)$ ), speed ( $\mathbb{E}(S)$ , km/h, assuming constant movement), and distance travelled ( $P(M) \times \mathbb{E}(S) = \mathbb{E}(D)$ , km/h) as estimated by models without and with temperature ( $\mathbb{E}(\dots|T)$ ), after post-stratifying to a 1-hour sampling rate and a temperature of  $T = 0^\circ\text{C}$ .

Species	$\hat{P}(M)$	$\hat{P}(M T)$	$\hat{\mathbb{E}}(S)$	$\hat{\mathbb{E}}(S T)$	$\hat{\mathbb{E}}(D)$	$\hat{\mathbb{E}}(D T)$
<i>C. canadensis</i>	0.16	0.17	0.57	0.57	0.09	0.10
<i>Canis lupus</i>	0.23	0.22	2.64	2.67	0.61	0.60
<i>O. americanus</i>	0.15	0.13	0.43	0.42	0.06	0.06
<i>Puma concolor</i>	0.27	0.31	0.74	0.76	0.20	0.24
<i>R. tarandus</i> (b)	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus</i> (sm)	0.11	0.11	0.43	0.42	0.05	0.05
<i>U. arctos horr.</i>	0.05	0.05	0.72	0.72	0.04	0.04

Near  $0^\circ\text{C}$ , wolves selected for dense forest cover ( $\gtrapprox 50\%$ ), elevations near 1 km, and distances from water  $< 10$  km; elk selected for forest cover near 50%, elevations between 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (< 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover, an elevation of  $\sim 1$  km, and distances from water  $< 10$  km; boreal caribou selected for intermediate to dense forest cover, elevations near 500 m, and distances from water  $< 10$  km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances from water  $< 5$  km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances from water  $< 2$  km.

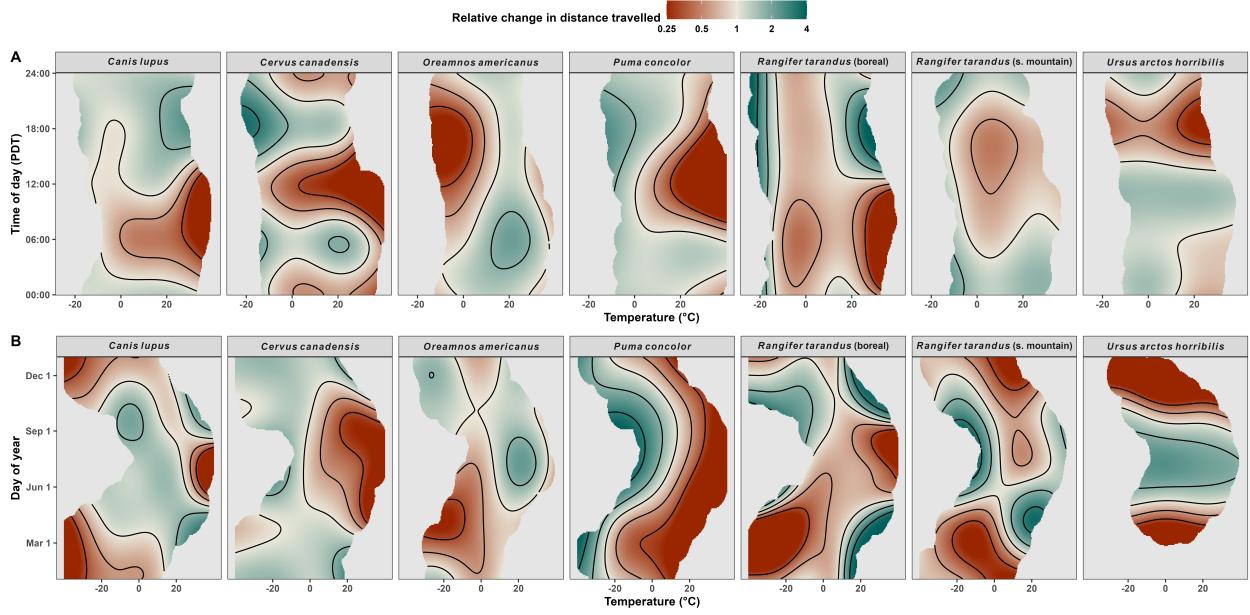
There was relatively strong agreement between models with and without temperature (Figs. B3, and B14), but including temperature always resulted in better fits. All analyses of deviance showed that temperature significantly affected movement behavior (all p-values  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC}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

292 **4.1 Effects of temperature on movement rates**

293 The effects of temperature on movement rates varied in both direction and magnitude across  
294 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
295 migration, hibernation; Figs. B4-B6). Smooth interaction terms were well-behaved and  
296 indicated clear shifts in activity over time of day and day of year for all species. The  
297 models had good in-sample prediction (Fig. B7) and explained reasonably high proportions  
298 of the deviance (79.3% for the Gamma model and 10.7% for the binomial model, which is  
299 relatively high for a binomial model with binary responses: see ch. 11 of McElreath (2020)].  
300 All species adapted their daily and seasonal movement behaviour to changes in temperature  
301 (Fig. 3). The clearest example of this was cougars. In mid summer, they moved mostly  
302 in the evening if temperatures were cool and mostly in the early morning if temperatures  
303 were hot. Throughout the year, they tended to move more when it was colder, but what  
304 they perceived as “colder” depended on the time of year. However, uncertainties around  
305 the estimated effects were often higher at extreme temperatures due to data scarcity. All  
306 species’ estimated probability of moving decreased with sampling intervals approximately  
307 above 1 hour, and most species’ estimated speed when moving decreased monotonically with  
308 sampling interval, although the estimated trends were highly uncertain for some species (Fig.  
309 B8).

310 **4.2 Effects of temperature on habitat selection**

311 Species’ relative selection strength (RSS) was generally strongest for elevation and weak-  
312 est for forest cover, but species’ RSS for resources depended on temperature (Fig. 4).  
313 Changes in RSS with temperature were also strongest for elevation and generally weak-  
314 est distance from water, but there were no common trends across all species for any of the  
315 three resources. All species, with the exception of cougars, exhibited a clear temperature-  
316 dependent shift in their preference for forest cover. At higher temperatures, wolves, mountain  
317 goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted



**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.

318 towards more intermediate forest cover without much of a change in preference width. All  
319 species shifted elevationally with temperature, although boreal caribou's selection strength  
320 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain  
321 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,  
322 and grizzly bears decreased in elevation. Most species generally remained within 5 km of  
323 water, and temperature did not affect their selection strength as much as for the other two  
324 resources. Again, estimated RSS values were generally most uncertain at extreme tempera-  
325 tures (Fig. B15).

### 326 4.3 Predicted changes in movement during the 21<sup>st</sup> century

327 The predicted changes in distance traveled varied across species in both direction and magni-  
328 tude, but worse climate-change SSPs always corresponded to greater absolute changes (Fig.  
329 5). Additionally, species that were predicted to move less often did not necessarily have lower  
330 speeds when moving, and vice versa (Figs. B9 and B10). Overall, absolute changes by 2100  
331 under the best-case SSP were small (approximately 0% to +4%), while under the worst-case

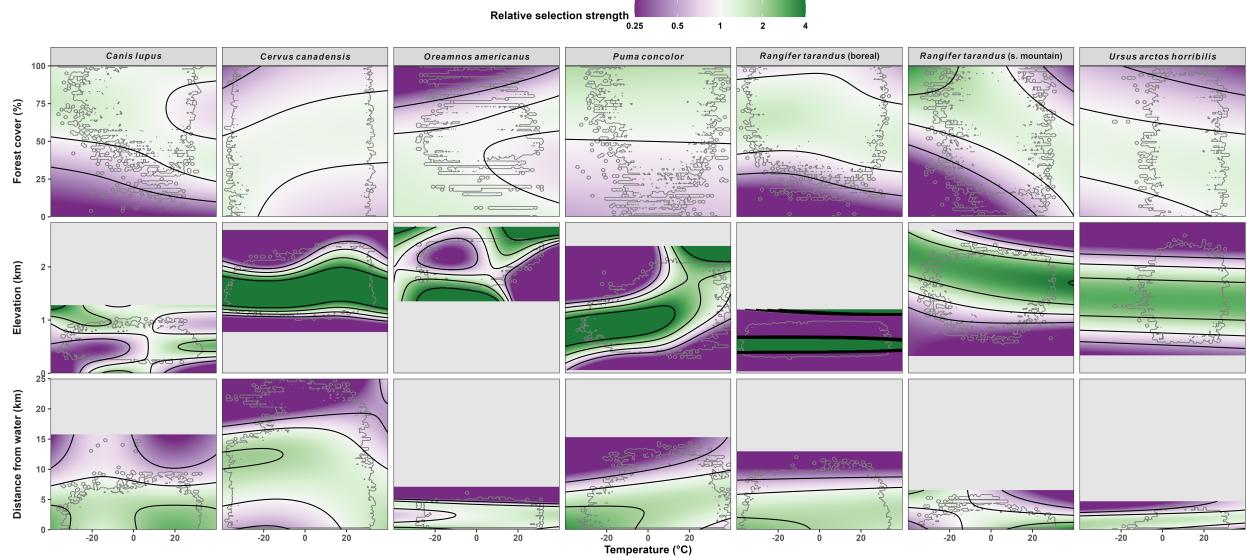


Figure 4: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed data. RSS values were re-centered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

332 SSP absolute changes ranged from ~2% (grizzly bears) to ~24% (cougars). Notably, while  
 333 the models estimated that grizzly bears would move substantially less (if at all) in winter  
 334 (Figs. 3, B4-B6), the models did not explicitly account for changes in hibernation phenol-  
 335 ogy. Consequently, the climate change projections do not explicitly account for changes in  
 336 energetic needs or physiology. Projected changes also varied spatially due to heterogeneity  
 337 in projected climate change (Fig. 6). Again, absolute changes were generally greatest under  
 338 worse SSPs, but the direction of change at each location also varied across SSPs (most visible  
 339 in cougars).

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

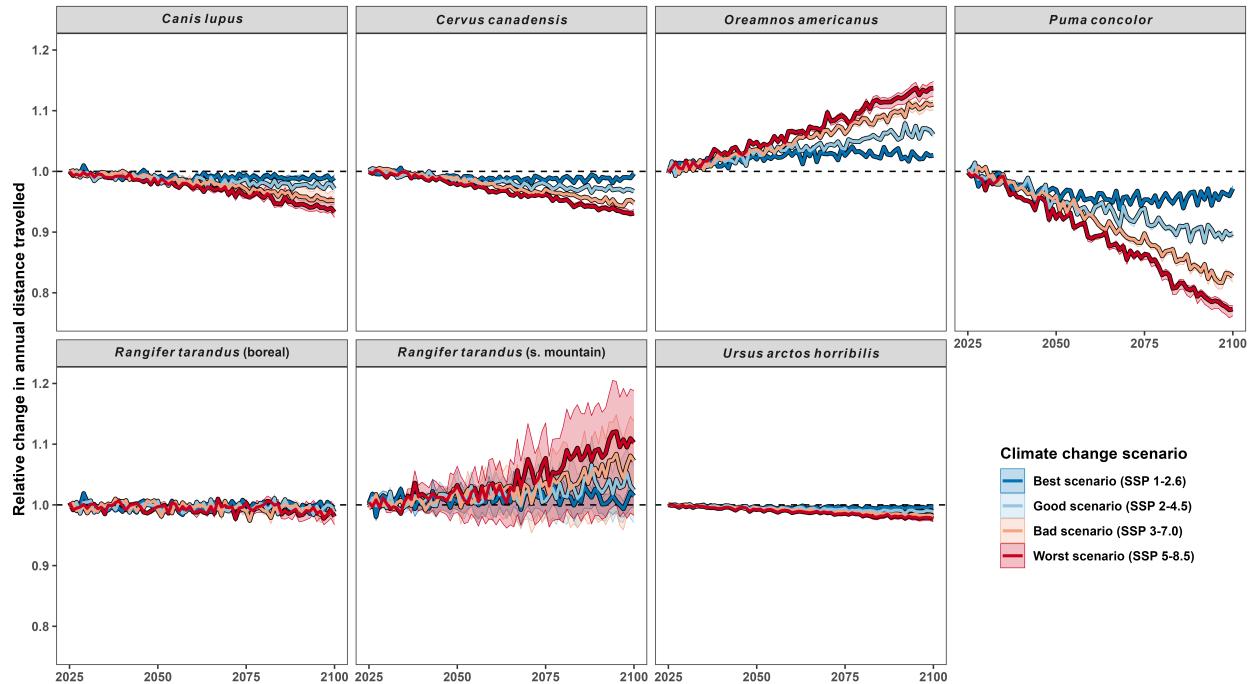
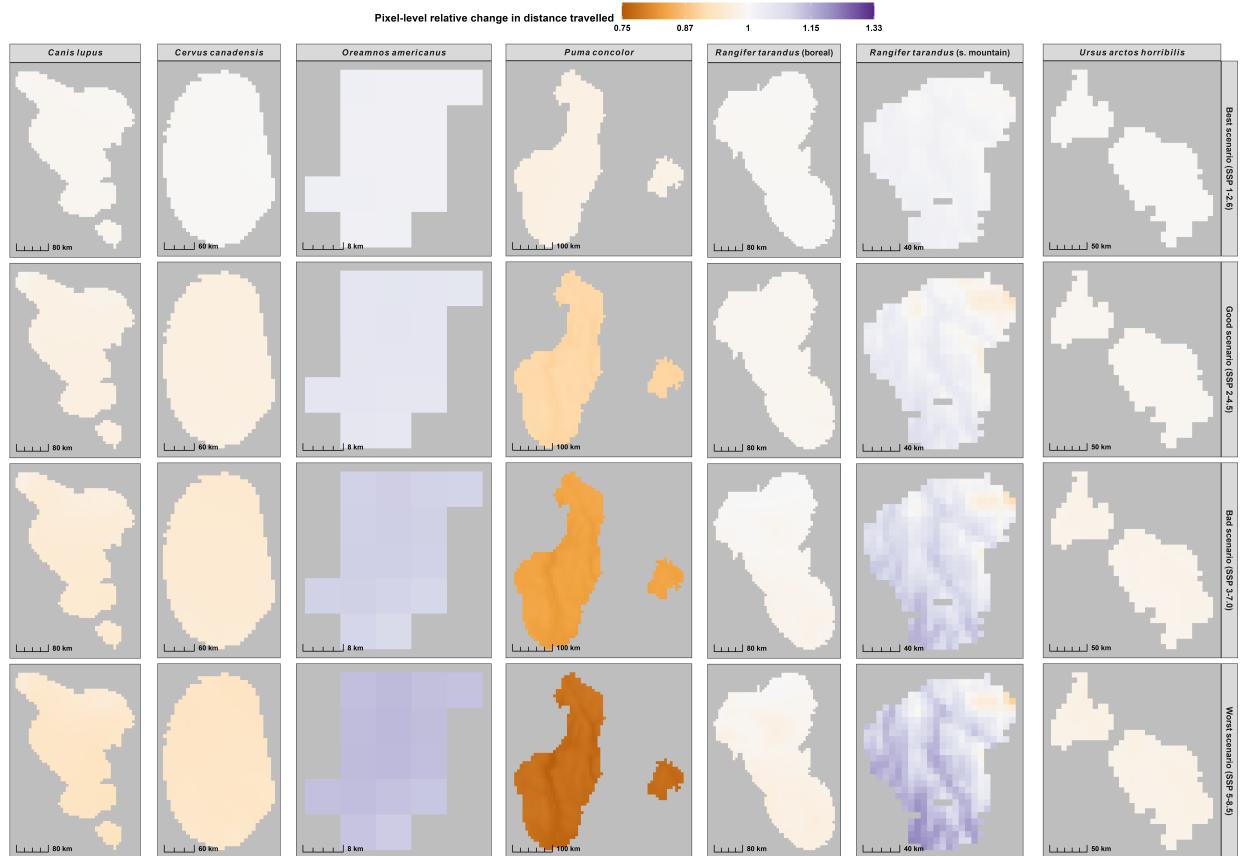


Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to 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.



**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).

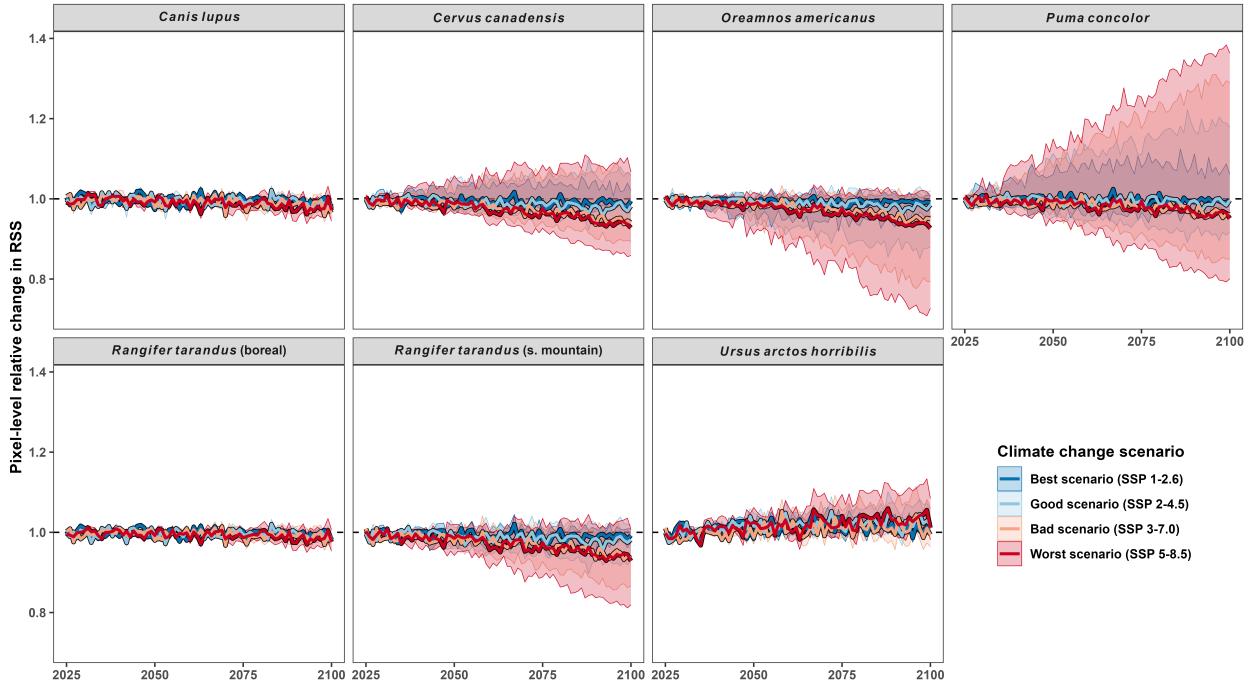
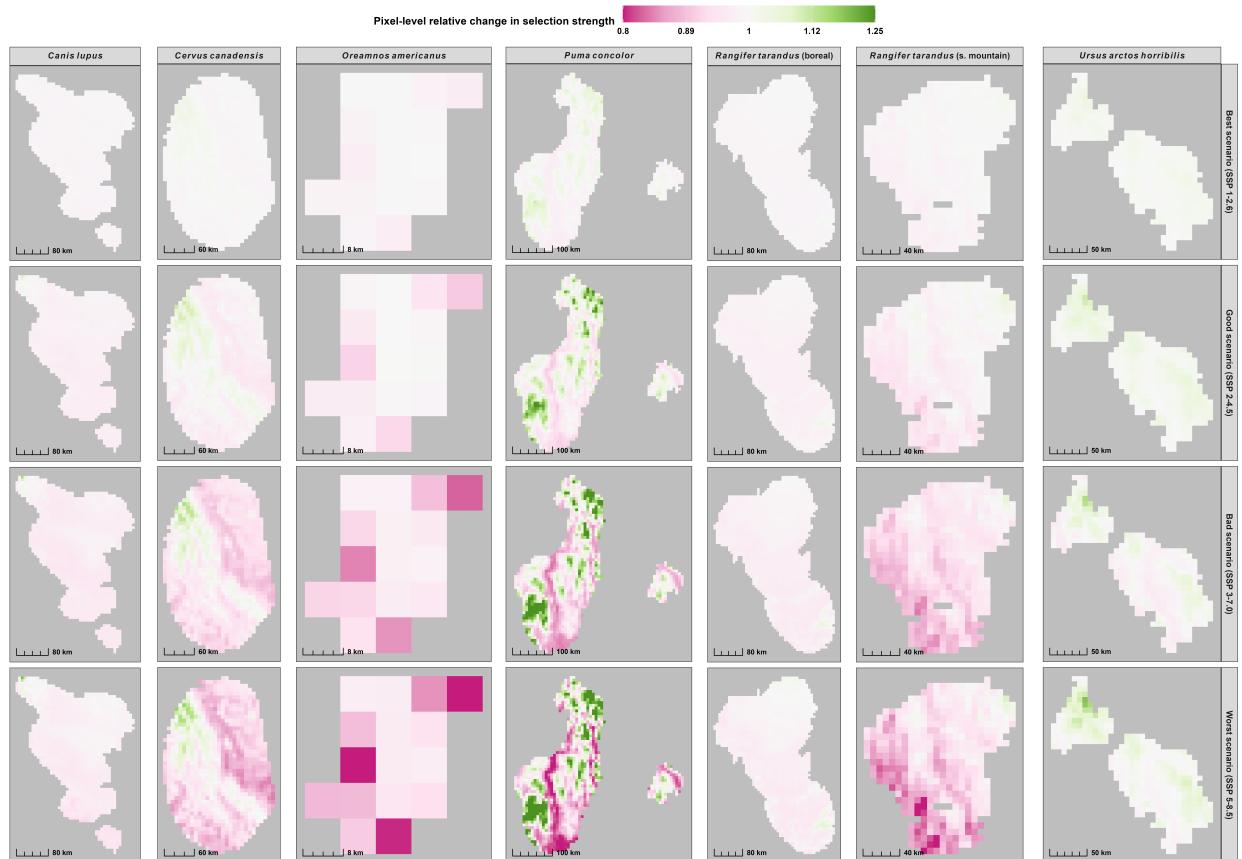


Figure 7: All species are expected to exhibit a decrease in median relative selection strength (RSS) for their current range, irrespective of climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in median RSS within each species' observed 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).

## 348 5 Discussion

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

356 Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3  
 357 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear.  
 358 At warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;  
 359 Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators,  
 360 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>361</sup> As extreme temperature events become more frequent and prolonged throughout the year  
<sup>362</sup> (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical be-  
<sup>363</sup> haviours that may alter community structures and behaviours, both during such events and  
<sup>364</sup> afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance,  
<sup>365</sup> changes in climate and phenology impact the life history and behaviour of many hibernat-  
<sup>366</sup> ing mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality  
<sup>367</sup> (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021).

<sup>368</sup> Changes in animal movement behavior may also alter the frequency and intensity of  
<sup>369</sup> human-wildlife conflict, especially with the addition of growing pressures from human de-  
<sup>370</sup> velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At  
<sup>371</sup> the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,  
<sup>372</sup> 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease  
<sup>373</sup> (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being  
<sup>374</sup> preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;  
<sup>375</sup> Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;  
<sup>376</sup> Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences  
<sup>377</sup> for population and ecosystem structures and dynamics as prey, predators, and competitors  
<sup>378</sup> experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*  
<sup>379</sup> *al.*, 2011).

<sup>380</sup> Our ability to respond changes in climate is contingent on our ability to prepare for and  
<sup>381</sup> predict change. However, predicting animal behaviour becomes increasingly complicated as  
<sup>382</sup> the conditions animals are exposed to deviate from current, typical conditions, especially  
<sup>383</sup> when responses are nonlinear and data are sparse. Consequently, we do not present our re-  
<sup>384</sup> sults as a definitive guide to how mammals in western Canada will respond to climate change.  
<sup>385</sup> Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement  
<sup>386</sup> rates and habitat selection depend on temperature and (2) how one can estimate mammals'  
<sup>387</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>414</sup> Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme  
<sup>415</sup> heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and  
<sup>416</sup> timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley,  
<sup>417</sup> 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at  
<sup>418</sup> the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially  
<sup>419</sup> since landscape changes will likely depend not only on the direct effect of temperature but  
<sup>420</sup> also on cascading changes in the availability and unpredictability of resources (McLellan &  
<sup>421</sup> McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

<sup>422</sup> **5.2 Effects of temperature on habitat selection**

<sup>423</sup> As with the effects of temperature on movement rates, the heterogeneity of temperature  
<sup>424</sup> effects on species' habitat selection indicates that efficient and proactive habitat conservation  
<sup>425</sup> will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
<sup>426</sup> physiological responses to temperature that may impact movement, such as changes in the  
<sup>427</sup> phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or  
<sup>428</sup> behaviour (e.g., migration, food caching), other than as direct responses to temperature.  
<sup>429</sup> Consequently, the behavioural changes we present should be interpreted carefully. While  
<sup>430</sup> some seasonal cycles do not depend directly on temperature and may thus not be impacted  
<sup>431</sup> directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the  
<sup>432</sup> predictions we present also rely on the assumption that mammals will not adapt these  
<sup>433</sup> seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage  
<sup>434</sup> availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important  
<sup>435</sup> to stress the distinction between habitat selection and quality. While animals tend to select  
<sup>436</sup> for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can  
<sup>437</sup> also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,  
<sup>438</sup> 2021).

<sup>439</sup> **5.3 Predicted changes in movement during the 21<sup>st</sup> century**

<sup>440</sup> Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on  
<sup>441</sup> Biological Diversity, 2022) will require careful planning but often also rapid action. In the  
<sup>442</sup> case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the  
<sup>443</sup> end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment  
<sup>444</sup> and Climate Change, 2024). Additionally, efficient and effective conservation will require  
<sup>445</sup> collaboration with Indigenous and local communities to ensure Treaties are respected in the  
<sup>446</sup> process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,  
<sup>447</sup> 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,  
<sup>448</sup> 2021).

<sup>449</sup> The diversity in predicted changes in movement behavior by 2100 (both across species  
<sup>450</sup> and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the  
<sup>451</sup> need for careful planning that incorporates not only reliable estimates of change but also  
<sup>452</sup> pragmatic and communicable measures of uncertainty and variability around such estimates.  
<sup>453</sup> For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-  
<sup>454</sup> individual variation should be accounted for when deciding the location and size of protected  
<sup>455</sup> areas (Jeltsch *et al.*, 2025). Population-level means that ignore such variation can greatly  
<sup>456</sup> limit the efficacy of conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024; Silva  
<sup>457</sup> *et al.*, 2025). Additionally, accurate estimates of the effects of changes in temperature on  
<sup>458</sup> mammals’ movement require a holistic view of the direct effects of temperature on mammals’  
<sup>459</sup> movement directly as well as its effects on other drivers of movement, such as forage and prey  
<sup>460</sup> availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*,  
<sup>461</sup> 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*,  
<sup>462</sup> 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation  
<sup>463</sup> among the responses of different species (and individuals), especially as populations undergo  
<sup>464</sup> a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from  
<sup>465</sup> human activity, including habitat fragmentation, habitat loss, and greater human presence

<sup>466</sup> in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal  
<sup>467</sup> *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and  
<sup>468</sup> likely decreases), some animals may disperse, relocate to a new habitat, or remain within  
<sup>469</sup> the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*,  
<sup>470</sup> 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

<sup>471</sup> **5.4 Species-specific considerations**

<sup>472</sup> **5.4.1 *Canis lupus***

<sup>473</sup> **5.4.2 *Cervus canadensis***

<sup>474</sup> **5.4.3 *Oreamnos americanus***

<sup>475</sup> **5.4.4 *Puma concolor***

<sup>476</sup> attraction for disconnected patches of high elevation could lead to fragmentation or traps

<sup>477</sup> **5.4.5 *Rangifer tarandus* (boreal)**

<sup>478</sup> Increasing temperatures increased RSS for both elevations near ~500 m as well as > 1,000  
<sup>479</sup> m, but such a selection is only possible if: (1) such habitats exist in the animals' range, and  
<sup>480</sup> (2) crossing the 500 m to > 1,000 m regions is safe and attractive

<sup>481</sup> **5.4.6 *Rangifer tarandus* (s. mountain)**

<sup>482</sup> HRSFs do not account for migratory behavior due to reproduction or predation risk

<sup>483</sup> **5.4.7 *Ursus arctos horribilis***

<sup>484</sup> **5.5 Considerations for future studies**

<sup>485</sup> Our work highlights three central considerations for future research: (1) telemetry sam-  
<sup>486</sup> pling rates should be designed primarily in relation to the movement timescales of the species

487 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of indi-  
488 viduals tracked and the length of each telemetry should depend not just on population size  
489 but also the rate of environmental change, and (3) predicting changes in movement behaviour  
490 becomes highly complex when responses are nonlinear, especially when changes depend on  
491 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses  
492 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

493 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,  
494 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-  
495 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.  
496 This dependency is because coarsely-sampled movement data contains information on large-  
497 scale movements (range crossings, migrations) but not fine-scale movements, including first-  
498 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour  
499 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-  
500 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement  
501 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional  
502 examples of how the frequency of location data affects the results that can be inferred by  
503 modeling movemet behavior. Consequently, we suggest being cautious when comparing esti-  
504 mated movement behaviours across species, even though all predictions have been corrected  
505 to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Ide-  
506 ally, sampling schedules should be fine enough to reconstruct animals' movement movement  
507 paths. Good estimates of an animal's speed and trajectory require telemetry locations to  
508 be taken more often than the animal's directional persistence (Noonan *et al.*, 2019a), so  
509 that, on average, the dataset contains multiple locations in between changes in direction.  
510 What constitutes a change in direction depends on what movement scale one is investigating.  
511 Small-scale movements and first-order spatial selection will require more frequent sampling  
512 than migratory movement or second-order and third-order spatial selection. While `ctmm`  
513 movement models are scale-invariant in that any model can be scaled to larger or smaller

514 areas and timescales, the model estimates are not independent of the scale of the sampling  
515 frequency.

516 When landscapes are relatively predictable across years, a larger number of sampled  
517 individuals is likely preferable over the duration of each tracking period. The greater number  
518 of tracked animals allows one to quantify the variance across individuals, including the  
519 range of conditions and environments that individual animals are in. A good estimate of  
520 inter-individual variance provides better coefficient estimates along with more appropriate  
521 measures of uncertainty. However, when conditions across years are stochastic, multi-year  
522 telemetries allow one to better estimate inter-annual variation without conflating it with  
523 inter-individual differences. Given the widespread, rapid, and accelerating changes across  
524 many habitats (particularly at high elevations and at high latitudes), we suggest researchers  
525 focus on long-term telemetry datasets to quantify the effects of intra-annual variability while  
526 increasing the ranges of temperatures each individual is observed in. Longer observational  
527 periods can also improve the chances of observing different community dynamics, such as  
528 shifts in predator-prey dynamics.

529 Temperature affects many aspects of mammalian physiology and behavior, including en-  
530 ergetics, sleep, and movement behavior. Climatic changes during the last two centuries have  
531 exposed many mammals to novel and increasingly extreme environmental conditions that  
532 have led to visible changes that impact not only individuals but also ecological and human  
533 communities. However, quantifying the effects of climate change is often complex, espe-  
534 cially as conditions become increasingly different and extreme events become increasingly  
535 common. Accurately quantifying the nonlinear effects of temperature on when, how, and  
536 where mammals move requires careful data collection and model design. We have presented  
537 a multi-species analysis of the effects of temperature on mammalian movement rates and  
538 habitat selection in hopes that other researchers can leverage this framework and models  
539 to expand our understanding of how temperature affects the movement behavior of other  
540 species, including smaller mammals, more elusive species, and non-mammal animals. Un-

derstanding of how temperature affects each species in a community will allow us to begin making community-level inferences of how temperature will affect intra-specific interactions from a movement behavior perspective (Nathan *et al.*, 2008, 2022; Martinez-Garcia *et al.*, 2020). While adopting such a perspective is surely not simple, it would result in more complete estimates of the effects of climate change on community ecology, particularly when species are exposed to rapid change in many important variables. Future work should explore the effects of temperature on movement behavior while accounting for finer-scale and species specific variables that were not accounted for in this study. Examples of these include temporally dynamic measures of forest type and age, canopy density, competitive pressures, forage availability, and predator avoidance, or environmental stochasticity. However, many of these data not available, so we also suggest that more work be done on quantifying such measures using spatiotemporally dynamic models and sufficiently fine resolutions.

## 6 Author contributions

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

559 **References**

- 560 Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) [Estimating space-](#)  
561 [use and habitat preference from wildlife telemetry data](#). *Ecography*, **31**, 140–160.
- 562 Alston JM, Joyce MJ, Merkle JA, Moen RA (2020) [Temperature shapes movement and](#)  
563 [habitat selection by a heat-sensitive ungulate](#). *Landscape Ecology*, **35**, 1961–1973.
- 564 Alston JM, Fleming CH, Kays R et al. (2022) [Mitigating pseudoreplication and bias in](#)  
565 [resource selection functions with autocorrelation-informed weighting](#). *Methods in Ecology*  
566 [and Evolution](#), 2041–210X.14025.
- 567 Anderson SC, Branch TA, Cooper AB, Dulvy NK (2017) [Black-swan events in animal pop-](#)  
568 [ulations](#). *Proceedings of the National Academy of Sciences*, **114**, 3252–3257.
- 569 Arechavala-Lopez P, Minguito-Frutos M, Follana-Berná G, Palmer M (2019) [Common octo-](#)  
570 [pus settled in human-altered Mediterranean coastal waters: From individual home range](#)  
571 [to population dynamics](#) (ed Durif C). *ICES Journal of Marine Science*, **76**, 585–597.
- 572 Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G (2018) [Effects of air temperature on](#)  
573 [habitat selection and activity patterns of two tropical imperfect homeotherms](#). *Animal*  
574 [Behaviour](#), **140**, 129–140.
- 575 Aven T, Kvaløy JT (2002) [Implementing the Bayesian paradigm in risk analysis](#). *Reliability*  
576 [Engineering & System Safety](#), **78**, 195–201.
- 577 Ayre KK, Landis WG (2012) [A Bayesian Approach to Landscape Ecological Risk Assessment](#)  
578 [Applied to the Upper Grande Ronde Watershed, Oregon](#). *Human and Ecological Risk*  
579 [Assessment: An International Journal](#), **18**, 946–970.
- 580 Bartashevich P, Herbert-Read JE, Hansen MJ, Dhellemmes F, Domenici P, Krause J, Ro-  
581 [manczuk P \(2024\) Collective anti-predator escape manoeuvres through optimal attack](#)  
582 [and avoidance strategies](#). *Communications Biology*, **7**, 1586.
- 583 Basu A, Culpepper J, Blagrave K, Sharma S (2024) [Phenological Shifts in Lake Ice Cover](#)  
584 [Across the Northern Hemisphere: A Glimpse Into the Past, Present, and the Future of](#)

- 585        Lake Ice Phenology. *Water Resources Research*, **60**, e2023WR036392.
- 586    Berger J, Hartway C, Gruzdev A, Johnson M (2018) Climate Degradation and Extreme Icing  
587        Events Constrain Life in Cold-Adapted Mammals. *Scientific Reports*, **8**, 1156.
- 588    Botero CA, Weissing FJ, Wright J, Rubenstein DR (2015) Evolutionary tipping points in  
589        the capacity to adapt to environmental change. *Proceedings of the National Academy of  
590        Sciences*, **112**, 184–189.
- 591    Brivio F, Apollonio M, Anderwald P, Filli F, Bassano B, Bertolucci C, Grignolio S (2024)  
592        Seeking temporal refugia to heat stress: Increasing nocturnal activity despite predation  
593        risk. *Proceedings of the Royal Society B: Biological Sciences*, **291**, 20231587.
- 594    Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory  
595        of ecology. *Ecology*, **85**, 1771–1789.
- 596    Bunnell FL, Kremsater LL, Wells RW (2011) Global Weirding in British Columbia: Cli-  
597        mate Change and the Habitat of Terrestrial Vertebrates. *Journal of Ecosystems and  
598        Management*, **12**.
- 599    Burnett M (2023) climatenaR: Tools to Access ClimateNA data.
- 600    Carbeck K, Wang T, Reid JM, Arcese P (2022) Adaptation to climate change through  
601        seasonal migration revealed by climatic versus demographic niche models. *Global Change  
602        Biology*, **28**, 4260–4275.
- 603    Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theoretical Population  
604        Biology*, **9**, 129–136.
- 605    Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS (2012) Human selection  
606        of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B:  
607        Biological Sciences*, **279**, 4407–4416.
- 608    Convention on Biological Diversity (2022) 15/4. Kunming-Montreal Global Biodiversity  
609        Framework.
- 610    Cunningham SJ, Gardner JL, Martin RO (2021) Opportunity costs and the response of  
611        birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, **19**,

- 612 300–307.
- 613 Czado C, Brechmann EC (2014) *Bayesian Risk Analysis*. In: *Risk - A Multidisciplinary*  
614 *Introduction* (eds Klüppelberg C, Straub D, Welpe IM), pp. 207–240. Springer Interna-  
615 tional Publishing, Cham.
- 616 Deb JC, Forbes G, MacLean DA (2020) *Modelling the spatial distribution of selected North*  
617 *American woodland mammals under future climate scenarios*. *Mammal Review*, **50**,  
618 440–452.
- 619 Desjardins SPA, Friesen TM, Jordan PD (2020) *Looking back while moving forward: How*  
620 *past responses to climate change can inform future adaptation and mitigation strategies*  
621 *in the Arctic*. *Quaternary International*, **549**, 239–248.
- 622 Dierauer JR, Allen DM, Whitfield PH (2021) *Climate change impacts on snow and stream-*  
623 *flow drought regimes in four ecoregions of British Columbia*. *Canadian Water Resources*  
624 *Journal / Revue canadienne des ressources hydriques*, **46**, 168–193.
- 625 Duncan C, Chauvenet ALM, McRae LM, Pettorelli N (2012) *Predicting the Future Impact*  
626 *of Droughts on Ungulate Populations in Arid and Semi-Arid Environments* (ed Seebacher  
627 F). *PLoS ONE*, **7**, e51490.
- 628 Dupont L, Thierry M, Zinger L, Legrand D, Jacob S (2024) *Beyond reaction norms: The*  
629 *temporal dynamics of phenotypic plasticity*. *Trends in Ecology & Evolution*, **39**, 41–51.
- 630 Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR (2023) *The travel speeds of large animals*  
631 *are limited by their heat-dissipation capacities* (ed Hedenström A). *PLOS Biology*, **21**,  
632 e3001820.
- 633 Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, Windels  
634 SK (2017) *Implications of the thermal environment for terrestrial wildlife management*.  
635 *Wildlife Society Bulletin*, **41**, 183–193.
- 636 Environment and Climate Change Canada (2024) *Canadian Environmental Sustainability*  
637 *Indicators: Canada's conserved areas*.
- 638 Falardeau M, Bennett EM, Else B et al. (2022) *Biophysical indicators and Indigenous and*

- 639 Local Knowledge reveal climatic and ecological shifts with implications for Arctic Char  
640 fisheries. *Global Environmental Change*, **74**, 102469.
- 641 Fjelldal MA, Wright J, Stawski C (2021) Nightly torpor use in response to weather conditions  
642 and individual state in an insectivorous bat. *Oecologia*, **197**, 129–142.
- 643 Fleming CH, Calabrese JM (2017) A new kernel density estimator for accurate home-range  
644 and species-range area estimation (ed Dray S). *Methods in Ecology and Evolution*, **8**,  
645 571–579.
- 646 Fleming CH, Calabrese JM (2023) Ctmm: Continuous-Time Movement Modeling.
- 647 Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF (2014) From  
648 Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement  
649 Modes across Spatiotemporal Scales. *The American Naturalist*, **183**, E154–E167.
- 650 Fuller A, Mitchell D, Maloney SK, Hetem RS (2016) Towards a mechanistic understanding  
651 of the responses of large terrestrial mammals to heat and aridity associated with climate  
652 change. *Climate Change Responses*, **3**, 10.
- 653 Gerlich HS, Loboda S, Simpson GL, Savage J, Schmidt NM, Holmstrup M, Høye TT (2025)  
654 Species' traits modulate rapid changes in flight time in high-Arctic muscid flies under  
655 climate change. *Proceedings of the Royal Society B: Biological Sciences*, **292**.
- 656 Gilbert SL, Hundertmark KJ, Person DK, Lindberg MS, Boyce MS (2017) Behavioral plasticity  
657 in a variable environment: Snow depth and habitat interactions drive deer movement  
658 in winter. *Journal of Mammalogy*, **98**, 246–259.
- 659 Giroux A, Ortega Z, Attias N, Desbiez ALJ, Valle D, Börger L, Rodrigues Oliveira-Santos  
660 LG (2023) Activity modulation and selection for forests help giant anteaters to cope with  
661 temperature changes. *Animal Behaviour*, **201**, 191–209.
- 662 Glass TW, Breed GA, Robards MD, Williams CT, Kielland K (2021) Trade-off between pre-  
663 dation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted  
664 mesocarnivore. *Animal Behaviour*, **175**, 163–174.
- 665 Gulland FMD, Baker JD, Howe M et al. (2022) A review of climate change effects on marine

- 666 mammals in United States waters: Past predictions, observed impacts, current research  
667 and conservation imperatives. *Climate Change Ecology*, **3**, 100054.
- 668 Hall LE, Chalfoun AD, Beever EA, Loosen AE (2016) Microrefuges and the occurrence of  
669 thermal specialists: Implications for wildlife persistence amidst changing temperatures.  
670 *Climate Change Responses*, **3**, 8.
- 671 Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM (2014) Fine-  
672 grain modeling of species' response to climate change: Holdouts, stepping-stones, and  
673 microrefugia. *Trends in Ecology & Evolution*, **29**, 390–397.
- 674 Hegel TM, Mysterud A, Huettmann F, Stenseth NC (2010) Interacting effect of wolves and  
675 climate on recruitment in a northern mountain caribou population. *Oikos*, **119**, 1453–  
676 1461.
- 677 Hersbach H, Bell B, Berrisford P et al. (2023) ERA5 hourly data on single levels from 1940  
678 to present.
- 679 Hessami MA, Bowles E, Popp JN, Ford AT (2021) Indigenizing the North American Model  
680 of Wildlife Conservation (ed Beazley K). *FACETS*, **6**, 1285–1306.
- 681 Hetem RS, Fuller A, Maloney SK, Mitchell D (2014) Responses of large mammals to climate  
682 change. *Temperature*, **1**, 115–127.
- 683 Hijmans RJ (2023) Terra: Spatial Data Analysis.
- 684 Hollister J, Shah T, Nowosad J, Robitaille AL, Beck MW, Johnson M (2023) Elevatr: Access  
685 Elevation Data from Various APIs.
- 686 Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D (2020) Cold and hungry:  
687 Combined effects of low temperature and resource scarcity on an edge-of-range temperate  
688 primate, the golden snub-nose monkey. *Ecography*, **43**, 1672–1682.
- 689 Huang M-T, Zhai P-M (2021) Achieving Paris Agreement temperature goals requires carbon  
690 neutrality by middle century with far-reaching transitions in the whole society. *Advances*  
691 in Climate Change Research, **12**, 281–286.
- 692 IPCC (2023) Climate Change 2021 – The Physical Science Basis: Working Group I Con-

- 693 tribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate  
694 Change, 1st edn. Cambridge University Press.
- 695 Jahn M, Seebacher F (2022) Variations in cost of transport and their ecological consequences:  
696 A review. *Journal of Experimental Biology*, **225**, jeb243646.
- 697 Jeltsch F, Roeleke M, Abdelfattah A et al. (2025) The need for an individual-based global  
698 change ecology. *Individual-based Ecology*, **1**, 1–18.
- 699 Jessen C (2001) Temperature Regulation in Humans and Other Mammals. Springer Berlin  
700 Heidelberg, Berlin, Heidelberg.
- 701 Johnson DH (1980) The Comparison of Usage and Availability Measurements for Evaluating  
702 Resource Preference. *Ecology*, **61**, 65–71.
- 703 Johnson HE, Lewis DL, Verzuh TL, Wallace CF, Much RM, Willmarth LK, Breck SW (2018)  
704 Human development and climate affect hibernation in a large carnivore with implications  
705 for human–carnivore conflicts (ed Bieber C). *Journal of Applied Ecology*, **55**, 663–672.
- 706 Kacelnik A, Krebs JR, Bernstein C (1992) The ideal free distribution and predator-prey  
707 populations. *Trends in Ecology & Evolution*, **7**, 50–55.
- 708 Kays R, Davidson SC, Berger M et al. (2022) The Movebank system for studying global  
709 animal movement and demography. *Methods in Ecology and Evolution*, **13**, 419–431.
- 710 Kienzle SW (2018) Has it become warmer in Alberta? Mapping temperature changes for  
711 the period 1950–2010 across Alberta, Canada. *Canadian Geographies / Géographies  
712 canadiennes*, **62**, 144–162.
- 713 Kohl MT, Ruth TK, Metz MC, Stahler DR, Smith DW, White PJ, MacNulty DR (2019) Do  
714 prey select for vacant hunting domains to minimize a multi-predator threat? (ed Gaillard  
715 J). *Ecology Letters*, **22**, 1724–1733.
- 716 Lamb CT, Willson R, Menzies AK et al. (2023) Braiding Indigenous rights and endangered  
717 species law. *Science*, **380**, 694–696.
- 718 Leclerc M, Leblond M, Le Corre M, Dussault C, Côté SD (2021) Determinants of migra-  
719 tion trajectory and movement rate in a long-distance terrestrial mammal (ed Reyna R).

- 720        *Journal of Mammalogy*, **102**, 1342–1352.
- 721    Levins RA (1974) Evolution in changing environments: Some theoretical explorations, 3.  
722        printing edn. Princeton Univ. Press, Princeton, NJ.
- 723    Li Z, Wood SN (2020) Faster model matrix crossproducts for large generalized linear models  
724        with discretized covariates. *Statistics and Computing*, **30**, 19–25.
- 725    Liu JA, Meléndez-Fernández OH, Bumgarner JR, Nelson RJ (2022) Effects of light pollution  
726        on photoperiod-driven seasonality. *Hormones and Behavior*, **141**, 105150.
- 727    Logares R, Nuñez M (2012) Black Swans in ecology and evolution: The importance of  
728        improbable but highly influential events. *Ideas in Ecology and Evolution*.
- 729    Malpeli KC (2022) Ungulate migration in a changing climate—An initial assessment of cli-  
730        mate impacts, management priorities, and science needs. Reston, VA.
- 731    Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM (2020) How range res-  
732        idency and long-range perception change encounter rates. *Journal of Theoretical Biology*,  
733        **498**, 110267.
- 734    Matthiopoulos J (2022) Defining, estimating, and understanding the fundamental niches of  
735        complex animals in heterogeneous environments. *Ecological Monographs*, **92**, e1545.
- 736    McCain CM (2019) Assessing the risks to United States and Canadian mammals caused  
737        by climate change using a trait-mediated model (ed Heske E). *Journal of Mammalogy*,  
738        gyz155.
- 739    McElreath R (2020) Statistical rethinking: A Bayesian course with examples in R and Stan,  
740        Second edition edn. CRC Press, Boca Raton London New York.
- 741    McLellan ML, McLellan BN (2015) Effect of Season and High Ambient Temperature on  
742        Activity Levels and Patterns of Grizzly Bears (*Ursus arctos*) (ed Crocker DE). *PLOS  
743        ONE*, **10**, e0117734.
- 744    McNab BK (1970) Body Weight and the Energetics of Temperature Regulation. *Journal of  
745        Experimental Biology*, **53**, 329–348.
- 746    Melin M, Matala J, Mehtätalo L, Pusenius J, Packalen T (2023) The effect of snow depth

- 747       on movement rates of GPS-collared moose. *European Journal of Wildlife Research*, **69**,  
748       21.
- 749       Merkle JA, Monteith KL, Aikens EO et al. (2016) Large herbivores surf waves of green-up  
750       during spring. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160456.
- 751       Mezzini S, Fleming CH, Medici EP, Noonan MJ (2025) How resource abundance and resource  
752       stochasticity affect organisms' range sizes. *Movement Ecology*, **13**, 20.
- 753       Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, Kauffman MJ  
754       (2018) Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, **127**, 1060–  
755       1068.
- 756       Minister of Environment and Climate Change (2024) An Act respecting transparency and ac-  
757       countability in relation to certain commitments Canada has made under the Convention  
758       on Biological Diversity.
- 759       Morley ID (2021) Spatiotemporal analysis of ecosystem change and landscape connectivity  
760       using satellite imagery in west-central British Columbia, Canada.
- 761       Mortlock E, Silovský V, Güldenpfennig J et al. (2024) Sleep in the wild: The importance  
762       of individual effects and environmental conditions on sleep behaviour in wild boar. *Pro-  
763       ceedings of the Royal Society B: Biological Sciences*, **291**, 20232115.
- 764       Mota-Rojas D, Titto CG, Orihuela A et al. (2021) Physiological and Behavioral Mechanisms  
765       of Thermoregulation in Mammals. *Animals*, **11**, 1733.
- 766       Muff S, Signer J, Fieberg J (2020) Accounting for individual-specific variation in habi-  
767       tat-selection studies: Efficient estimation of mixed-effects models using Bayesian or fre-  
768       quentist computation (ed Wal EV). *Journal of Animal Ecology*, **89**, 80–92.
- 769       Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A  
770       movement ecology paradigm for unifying organismal movement research. *Proceedings of  
771       the National Academy of Sciences*, **105**, 19052–19059.
- 772       Nathan R, Monk CT, Arlinghaus R et al. (2022) Big-data approaches lead to an increased  
773       understanding of the ecology of animal movement. *Science*, **375**, eabg1780.

- 774 Newediuk L, Richardson ES, Biddlecombe BA et al. (2024) Climate change, age acceleration,  
775 and the erosion of fitness in polar bears.
- 776 Noonan MJ, Tucker MA, Fleming CH et al. (2019b) A comprehensive analysis of autocor-  
777 relation and bias in home range estimation. *Ecological Monographs*, **89**, e01344.
- 778 Noonan MJ, Fleming CH, Akre TS et al. (2019a) Scale-insensitive estimation of speed and  
779 distance traveled from animal tracking data. *Movement Ecology*, **7**, 35.
- 780 Pease BS (2024) Ecological scales of effect vary across space and time. *Ecography*, **2024**,  
781 e07163.
- 782 Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models  
783 in ecology: An introduction with mgcv. *PeerJ*, **7**, e6876.
- 784 Pedersen SH, Bentzen TW, Reinking AK et al. (2021) Quantifying effects of snow depth on  
785 caribou winter range selection and movement in Arctic Alaska. *Movement Ecology*, **9**,  
786 48.
- 787 Peterson AN, Soto AP, McHenry MJ (2021) Pursuit and Evasion Strategies in the Predator–  
788 Prey Interactions of Fishes. *Integrative and Comparative Biology*, **61**, 668–680.
- 789 Pigeon KE, Stenhouse G, Côté SD (2016) Drivers of hibernation: Linking food and weather  
790 to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology*, **70**, 1745–  
791 1754.
- 792 Polazzo F, Limberger R, Pennekamp F, Ross SRP-J, Simpson GL, Petchey OL (2024) Mea-  
793 suring the Response Diversity of Ecological Communities Experiencing Multifarious En-  
794 vironmental Change. *Global Change Biology*, **30**, e17594.
- 795 Powers DR, Langland KM, Wethington SM, Powers SD, Graham CH, Tobalske BW (2017)  
796 Hovering in the heat: Effects of environmental temperature on heat regulation in foraging  
797 hummingbirds. *Royal Society Open Science*, **4**, 171056.
- 798 R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foun-  
799 dation for Statistical Computing, Vienna, Austria.
- 800 Riahi K, Vuuren DP van, Kriegler E et al. (2017) The Shared Socioeconomic Pathways and

- 801 their energy, land use, and greenhouse gas emissions implications: An overview. *Global*  
802 *Environmental Change*, **42**, 153–168.
- 803 Rice WL (2022) The conspicuous consumption of wilderness, or leisure lost in the wilderness.  
804 *World Leisure Journal*, **64**, 451–468.
- 805 Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and  
806 shape (with discussion). *Journal of the Royal Statistical Society: Series C (Applied*  
807 *Statistics)*, **54**, 507–554.
- 808 Rosenthal J, Booth R, Carolan N et al. (2022) The impact of recreational activities on  
809 species at risk in Canada. *Journal of Outdoor Recreation and Tourism*, **40**, 100567.
- 810 Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009) Identifying and prioritizing ungulate  
811 migration routes for landscape-level conservation. *Ecological Applications*, **19**, 2016–2025.
- 812 Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL (2019) Migratory plastic-  
813 ity is not ubiquitous among large herbivores (ed Chapman J). *Journal of Animal Ecology*,  
814 **88**, 450–460.
- 815 Schmidt NM, Grøndahl C, Evans AL et al. (2020) On the interplay between hypothermia  
816 and reproduction in a high arctic ungulate. *Scientific Reports*, **10**, 1514.
- 817 Schwerdt L, De Villalobos AE, Ferretti N (2024) Ecological niche modelling and thermal  
818 parameters to assess the prevalence of an endemic tarantula: The endurance of Gram-  
819 mostola vachoni Schiapelli & Gerschman, 1961. *Journal of Insect Conservation*.
- 820 Sherwood SC, Huber M (2010) An adaptability limit to climate change due to heat stress.  
821 *Proceedings of the National Academy of Sciences*, **107**, 9552–9555.
- 822 Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-  
823 induced rapid environmental change: Behaviour and evolution. *Evolutionary Applica-*  
824 *tions*, **4**, 367–387.
- 825 Silva I, Fleming CH, Noonan MJ, Fagan WF, Calabrese JM (2025) Too few, too many, or  
826 just right? Optimizing sample sizes for population-level inferences in animal tracking  
827 projects.

- 828 Slatyer RA, Umbers KDL, Arnold PA (2022) Ecological responses to variation in seasonal  
829 snow cover. *Conservation Biology*, **36**, e13727.
- 830 Smith BJ, MacNulty DR, Stahler DR, Smith DW, Avgar T (2023) Density-dependent habitat  
831 selection alters drivers of population distribution in northern Yellowstone elk. *Ecology*  
832 Letters, **26**, 245–256.
- 833 Stasinopoulos MD, Rigby RA (2007) Generalized additive models for location scale and  
834 shape (GAMLSS) in R. *Journal of Statistical Software*, **23**.
- 835 Steixner-Kumar S, Gläscher J (2020) Strategies for navigating a dynamic world. *Science*,  
836 **369**, 1056–1057.
- 837 Sullender BK, Cunningham CX, Lundquist JD, Prugh LR (2023) Defining the danger zone:  
838 Critical snow properties for predator–prey interactions. *Oikos*, **2023**, e09925.
- 839 Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R (2021) An overview of  
840 ecological traps in marine ecosystems. *Frontiers in Ecology and the Environment*, **19**,  
841 234–242.
- 842 Tan M, Zhang S, Stevens M, Li D, Tan EJ (2024) Antipredator defences in motion: Animals  
843 reduce predation risks by concealing or misleading motion signals. *Biological Reviews*,  
844 **99**, 778–796.
- 845 Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial loco-  
846 motion. I. Metabolic energy consumption as a function of speed and body size in birds  
847 and mammals. *Journal of Experimental Biology*, **97**, 1–21.
- 848 Tórrez-Herrera LL, Davis GH, Crofoot MC (2020) Do Monkeys Avoid Areas of Home Range  
849 Overlap Because They Are Dangerous? A Test of the Risk Hypothesis in White-Faced  
850 Capuchin Monkeys (*Cebus capucinus*). *International Journal of Primatology*, **41**, 246–  
851 264.
- 852 Tuanmu M, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and  
853 ecosystem modelling. *Global Ecology and Biogeography*, **23**, 1031–1045.
- 854 Tucker MA, Böhning-Gaese K, Fagan WF et al. (2018) Moving in the Anthropocene: Global

- reductions in terrestrial mammalian movements. *Science*, **359**, 466–469.
- Turner NJ, Clifton H (2009) “It’s so different today”: Climate change and indigenous lifeways in British Columbia, Canada. *Global Environmental Change*, **19**, 180–190.
- Tysor CS (2025) Countergradient variation in lodgepole pine flowering phenology.
- Verzuh TL, Rogers SA, Mathewson PD et al. (2023) Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales. *Journal of Animal Ecology*, **92**, 619–634.
- Walker WH, Meléndez-Fernández OH, Nelson RJ, Reiter RJ (2019) Global climate change and invariable photoperiods: A mismatch that jeopardizes animal fitness. *Ecology and Evolution*, **9**, 10044–10054.
- Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM (2022) Life history consequences of climate change in hibernating mammals: A review. *Ecography*, **2022**, e06056.
- Weststrate DK, Chhen A, Mezzini S, Safford K, Noonan MJ (2024) How climate change and population growth will shape attendance and human-wildlife interactions at British Columbia parks. *Journal of Sustainable Tourism*, 1–15.
- Williams JE, Blois JL (2018) Range shifts in response to past and future climate change: Can climate velocities and species’ dispersal capabilities explain variation in mammalian range shifts? *Journal of Biogeography*, **45**, 2175–2189.
- Wilson RS, Franklin CE, Davison W, Kraft P (2001) Stenotherms at sub-zero temperatures: Thermal dependence of swimming performance in Antarctic fish. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **171**, 263–269.
- Winter VA, Smith BJ, Berger DJ et al. (2024) Forecasting animal distribution through individual habitat selection: Insights for population inference and transferable predictions. *Ecography*, e07225.
- Wong C, Ballegooien K, Ignace L, Johnson MJ(Gùdia), Swanson H (2020) Towards reconciliation: 10 Calls to Action to natural scientists working in Canada (ed Boran I). *FACETS*, **5**, 769–783.

- 882 Wood SN (2017) Generalized additive models: An introduction with R, Second edition edn.  
883 CRC Press/Taylor & Francis Group, Boca Raton.
- 884 Wood SN, Goude Y, Shaw S (2015) Generalized additive models for large data sets. *Journal*  
885 *of the Royal Statistical Society: Series C (Applied Statistics)*, **64**, 139–155.
- 886 Wood SN, Li Z, Shaddick G, Augustin NH (2017) Generalized Additive Models for Gigadata:  
887 Modeling the U.K. Black Smoke Network Daily Data. *Journal of the American Statistical*  
888 *Association*, **112**, 1199–1210.
- 889 Woo-Durand C, Matte J-M, Cuddihy G, McGourdji CL, Venter O, Grant JWA (2020) In-  
890 creasing importance of climate change and other threats to at-risk species in Canada.  
891 *Environmental Reviews*, **28**, 449–456.
- 892 Wright CA (2024) Survival and movements of mule deer (*Odocoileus hemionus*) in southern  
893 British Columbia. {PhD} {Thesis}, University of British Columbia.
- 894 Xu F, Si Y (2019) The frost wave hypothesis: How the environment drives autumn departure  
895 of migratory waterfowl. *Ecological Indicators*, **101**, 1018–1025.
- 896 Xu W, Barker K, Shawler A et al. (2021) The plasticity of ungulate migration in a changing  
897 world. *Ecology*, **102**, e03293.
- 898 Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, Chen X (2022) Emergence of  
899 universal scaling in weather extreme events.
- 900 Zhang X, Zhou T, Zhang W et al. (2023) Increased impact of heat domes on 2021-like heat  
901 extremes in North America under global warming. *Nature Communications*, **14**, 1690.
- 902 Zuñiga-Palacios J, Zuria I, Castellanos I, Lara C, Sánchez-Rojas G (2021) What do we know  
903 (and need to know) about the role of urban habitats as ecological traps? Systematic  
904 review and meta-analysis. *Science of The Total Environment*, **780**, 146559.
- 905 Zurowski M (2023) The summer Canada burned: The wildfire season that shocked the world.  
906 Postmedia / Greystone Books, Vancouver.