

The heat is on: Rising temperatures alter when, how, and where  
large terrestrial mammals move

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**Article type:** Research article

**Words in abstract:** 273

**Words in main text:** 7001

**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

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have quantitatively estimated the effects of temperature on mammalian movement behaviour, but few have estimated the effects of future climate change. 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 probability of moving, the speed when moving, and the habitat selection of six species throughout British Columbia, Canada, between 1998 and 2023. We show that temperature is a strong determinant of when, how, and where mammals move, and we predict that climate change will impact mammals' movement rates and habitat selection as temperatures warm throughout the 21<sup>st</sup> century. We found the effects of temperature on movement rates varied across species, so we suggest that species' estimated responses be interpreted holistically when making inferences about how climate change will impact ecological communities. In contrast, habitat selection strength decreased for all species within their observed ranges, suggesting that all six species may shift their range in the coming decades. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behavior and community structure will become crucial for effective and proactive conservation. We thus conclude by providing suggestions for conservation and future research, with particular attention to the study design, statistical modeling, and forecasting. We provide detailed R code and appendices so that other researchers can implement our methods on their own datasets.

## <sup>1</sup> 1 Introduction

<sup>2</sup> For most animals, movement is a rapid and low-cost response to a variety of stimuli (Nathan  
<sup>3</sup> *et al.*, 2008). Animals move to maximize resource availability (e.g., food, water, shelter, see:  
<sup>4</sup> Charnov, 1976; Kacelnik *et al.*, 1992), optimize habitat use (Winter *et al.*, 2024), and escape  
<sup>5</sup> predation (Peterson *et al.*, 2021; Bartashevich *et al.*, 2024; Tan *et al.*, 2024). However,  
<sup>6</sup> ambient temperature affects mammals' movement rates by altering the energetic cost of  
<sup>7</sup> movement (McNab, 1970; Taylor *et al.*, 1982; Brown *et al.*, 2004; Fuller *et al.*, 2016; Jahn  
<sup>8</sup> & Seebacher, 2022) and the risk of overheating (Hetem *et al.*, 2014; Dyer *et al.*, 2023).  
<sup>9</sup> Animals may search for a short-term buffer from extreme heat or cold via thermal refugia  
<sup>10</sup> (Hannah *et al.*, 2014; Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019;  
<sup>11</sup> Gulland *et al.*, 2022), which may even be preferred over forage abundance (e.g., Hall *et al.*,  
<sup>12</sup> 2016). Additionally, temperature also has indirect effects on movement through other drivers  
<sup>13</sup> of movement behaviour, such as trophic interactions (Hegel *et al.*, 2010), snow depth and  
<sup>14</sup> density (Montgomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and the frequency  
<sup>15</sup> and intensity of extreme events (Bunnell *et al.*, 2011; Zhang *et al.*, 2023), including forest  
<sup>16</sup> fires, droughts, and novel phenology (Bunnell *et al.*, 2011; Duncan *et al.*, 2012; Merkle *et*  
<sup>17</sup> *al.*, 2016; Slatyer *et al.*, 2022; Zurowski, 2023). Changes in temperature thus affects how  
<sup>18</sup> animals move (e.g., movement frequency and speed – their movement behaviour: Nathan *et*  
<sup>19</sup> *al.*, 2008; Dyer *et al.*, 2023) and where they move to (i.e., their habitat selection: Merkle *et*  
<sup>20</sup> *al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*, 2023).

<sup>21</sup> By impacting animal movement behavior, temperature also affects the consequences of  
<sup>22</sup> movement, such as encounter rates with resources (Mezzini *et al.*, 2025), other animals  
<sup>23</sup> (Martinez-Garcia *et al.*, 2020), and humans (Weststrate *et al.*, 2024), and these changes are  
<sup>24</sup> exacerbated at extreme temperatures (Wilson *et al.*, 2001; Berger *et al.*, 2018; Giroux *et al.*,  
<sup>25</sup> 2023). But what counts as “extreme” varies across species: Species that experience narrow  
<sup>26</sup> temperature ranges tend to be more sensitive to changes (e.g., giant anteaters, *Myrmecophaga*

*tridactyla*: Giroux *et al.*, 2023), while thermal generalists can adapt more easily to change (Levins, 1974; Botero *et al.*, 2015; Dupont *et al.*, 2024). However, generalists' greater adaptability is tested when they are subject to changes that are more severe (McCain, 2019), affect many factors (e.g., temperature, phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to respond within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016; Xu *et al.*, 2021).

In the last 200 years, many ecosystems experienced widespread warming that resulted in milder and shorter winters, hotter and longer summers, and a greater risk of extremely high temperatures (IPCC, 2023). Over the next 100 years, these changes are expected to worsen and continue to impact mammals' fitness, movement behaviour, and habitat selection as animals cope with growing heat stress (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020) and more frequent and intense extreme events (Bunnell *et al.*, 2011), along with increasing anthropogenic pressure (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Weststrate *et al.*, 2024). Consequently, it remains unclear how or whether species will be able to respond to climate change in the current century (Deb *et al.*, 2020; Woo-Durand *et al.*, 2020; Verzuh *et al.*, 2023), especially when populations fail to adapt to changes (Botero *et al.*, 2015; Sawyer *et al.*, 2019) or are physiologically incapable to do so (Sherwood & Huber, 2010; Williams & Blois, 2018). Uncertainty in future conditions and their consequences on ecosystems present a need for a comprehensive understanding of (1) the direct effects of temperature on animal movement behaviour and (2) the implications such changes and uncertainty will have on populations and species' adaptability and resiliency, as well as overall community structure. Recent work has documented the effects of climate change on mammals' ranges (Leclerc *et al.*, 2021), movement behaviour (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (e.g., body size, activity time, and elevational and latitudinal distribution McCain, 2019). However, it is still unclear how mammals will adapt their small-scale movement and habitat selection to changes in temperature during the 21<sup>st</sup> century (IPCC, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024).

54 Understanding the direct and indirect impacts of temperature on mammalian movement  
55 is essential for decision makers to respond to change in a proactive manner (Sawyer *et al.*,  
56 2009; McCain, 2019). The Canadian province of British Columbia is currently experiencing  
57 rapid widespread warming (Turner & Clifton, 2009; Dierauer *et al.*, 2021), phenological shifts  
58 (Basu *et al.*, 2024; Tysor, 2025), and more frequent and intense extreme events (Zhang *et*  
59 *al.*, 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the  
60 “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands and  
61 oceans by 2030 (Convention on Biological Diversity, 2022), decision makers must understand  
62 which areas will be of greatest value for maximizing the project’s effectiveness. Predicting  
63 how climate change will affect how, when, and where animals will move is necessary for  
64 identifying landscape dynamics and value will evolve throughout the century. Failing to  
65 understand how changes in temperature will affect mammalian movement behaviour and  
66 habitat selection will hinder our ability to respond to the current climate crisis and make  
67 decisions that are viable in the long term.

68 This paper provides a framework for quantifying the effects of proximal air temperature  
69 on animal movement using quantitative methods that are flexible and statistically robust.  
70 We present results for six large-bodied terrestrial mammal species in British Columbia (BC),  
71 Canada (wolves: *Canis lupus*, elk: *Cervus canadensis*, mountain goats: *Oreamnos ameri-*  
72 *canus*, cougars: *Puma concolor*, boreal and southern mountain caribou: *Rangifer tarandus*,  
73 and grizzly bears: *Ursus arctos horribilis*; Table 1). Using over 25 years of telemetry data  
74 throughout a large spatial range of British Columbia and hourly air temperature data, we es-  
75 timate how these mammals altered their probability of movement, speed when moving, and  
76 habitat selection in response to temperature. We then pair the estimated responses with  
77 climate change projections to forecast the species’ movement during the 21<sup>st</sup> century un-  
78 der different climate-change scenarios (referred to as Shared Socioeconomic Pathways, SSP,  
79 Riahi *et al.*, 2017). We disentangle the direct and indirect effects of temperature on the  
80 movement behaviour of terrestrial mammals and discuss the consequences of these changes

81 at the individual, population, and community levels.

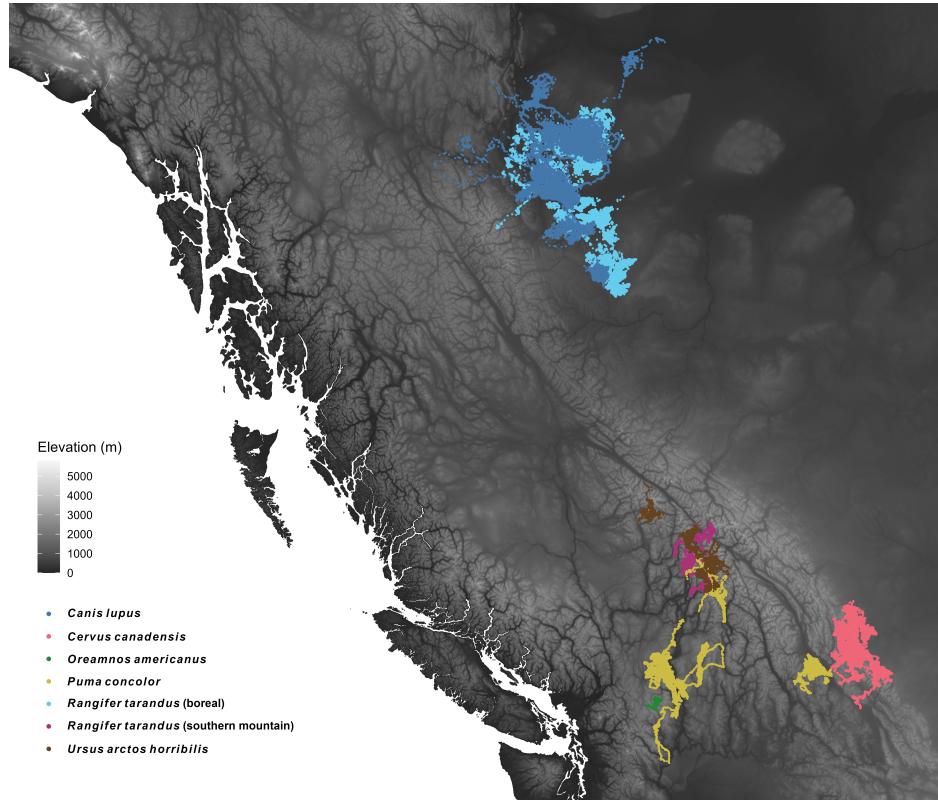


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

Table 1: Start and end of the GPS telemetries 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
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	18

82 **2 Methods**

83 **2.1 Datasets used**

84 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry  
85 data (Fig. 1); (2) historical hourly reanalyzed air temperature from the ERA5 dataset from  
86 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent  
87 forest cover, elevation, and distance from water; and (4) climate change projections under  
88 four Shared Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). While we acknowledge  
89 that forest type, structure, and age are important variables, we do not include such variables  
90 in this study for the sake of parsimony and comparability across species. We detail the data  
91 sources and analyses in the sections below.

92 **2.1.1 GPS telemetry data**

93 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank  
94 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou  
95 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public BC Oil and  
96 Gas Research and Innovation Society repository ([https://www.bcgoris.ca/projects/boreal-](https://www.bcgoris.ca/projects/boreal-caribou-telemetry-data)  
97 **MISSING INFO ON OTHER TELEMETRY DATA.**)  
98 From the full set of telemetry data, a total of 2396 GPS locations (0.16%, including col-  
99 lar calibration data) were removed using diagnostic plots of (1) distance from the median  
100 location, (2) straight-line displacement between locations, (3) turning angle, and (4) time  
101 interval between consecutive points. Particular attention was paid to points with large turn-  
102 ing angles ( $\gtrapprox 170^\circ$ ) and excessively high straight-line displacement, especially if antecedent  
103 and subsequent points indicated stationary behaviour (Appendix A).

104 **2.1.2 Historical temperature data and temperature projections**

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

111 We obtained rasters of projected monthly average temperature at a  $0.08^\circ$  resolution in  
112 BC from 2020 to 2100 under the different SSPs via the `climatenar` package (version 1.0,  
113 Burnett, 2023) for `R`. Since the climate projections only provided monthly means and ranges  
114 but no measures of variance or distributional assumptions, we used the hourly ERA5 data for  
115 BC from 1998 to 2023 (extremes included, Hersbach *et al.*, 2023) to calculate within-month  
116 variance in temperature, which we defined as the variance within a given pixel, month, and  
117 year. We then modeled the estimated variance using a GAM for location and scale (GAMLS,  
118 Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017).  
119 The linear predictor for the location (i.e., the mean) included smooth terms of the within-  
120 pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-  
121 dimensional smooth of space, and a tensor interaction product term of space and month. The  
122 linear predictor for the scale term (which governs the mean-variance relationship) included  
123 smooth terms of the monthly mean, month, and space. We did not include a smooth of year  
124 to avoid unrealistic projections when extrapolating beyond the range of historical data.

125 We simulated hourly variation in future weather by assuming hourly temperature fol-  
126 lowed a normal distribution with mean specified by the monthly `climatenar` climate pro-  
127 jections and variance as specified by the Gamma GAMLS. For each month within each year  
128 from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to  
129 the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the  
130 (normalized) Gaussian probability density for each quantile.

131 **2.1.3 Resource rasters**

132 We estimated percent forest cover and distance from water using the rasters created by  
133 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally  
134 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous  
135 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the  
136 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover  
137 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the  
138 nearest pixel with water using the `distance()` function from the `terra` package. Finally,  
139 we obtained two digital elevation models using the `get_elev_raster()` function from the  
140 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom  
141 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate  
142 change projections via `climatenar`. All final rasters and code are available on GitHub at  
143 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

144 **2.2 Estimating mammals' instantaneous speeds**

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

152 Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-  
153 gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
154 minimum instantaneous speed could be 0. We performed this correction by subtracting  
155 each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
156 used is available on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

157 [temperature/blob/main/functions/detrend\\_speeds.R](#). To avoid artifacts due to excessively  
158 small, non-zero speeds, we determined whether an animal was moving or not using a  $k$ -means  
159 algorithm with 2 clusters for each species' detrended speeds. When the algorithm clearly  
160 failed to discriminate between states, we estimated the split point using the inflection points  
161 in histograms of the detrended speeds (Fig. B1).

## 162 2.3 Estimating the effects of temperature on mammals' movement

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

### 168 2.3.1 Disentangling direct and indirect effects

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

180 Indirect effects of temperature also include all effects that can be controlled by altering  
181 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022). For example, in Fig.

182 2B, an increase in temperature may push an animal to prefer higher forest cover in search of  
 183 shade, and conservationists can mitigate these indirect effects of temperature by increasing  
 184 the availability of forested areas, since the effect of temperature on movement is conditional  
 185 on forest cover availability. In contrast, the animal may avoid moving if temperatures are  
 186 above 35°C, irrespective of its geographic and environmental space (*sensu* Matthiopoulos,  
 187 2022). In this case, it is not possible to mitigate the effects of temperature on movement  
 188 behaviour (other than changing temperature directly).

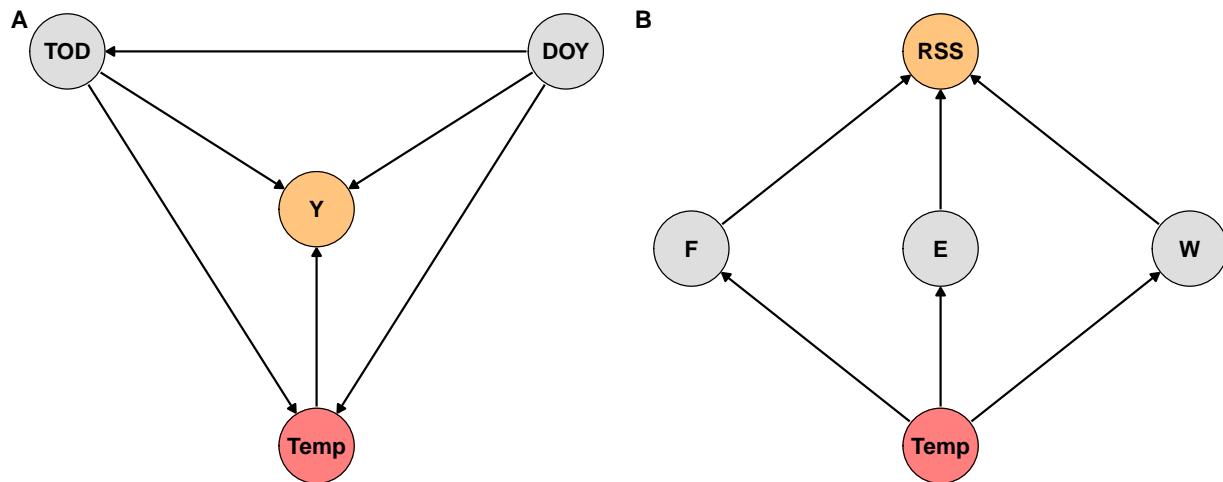


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled ( $Y$ ) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction 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.

### 189 2.3.2 Effects of temperature on movement rates

190 We estimated the effects of temperature (°C) on mammals' instantaneous movement state  
 191 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models  
 192 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R  
 193 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was  
 194 moving,  $P(M)$ , with a binomial family of distributions and logit link function. The response  
 195 variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an  
 196 animal's speed when moving (`speed`) with a gamma family of distributions and log link

197 function.

198 The HGAMs included random intercepts for each animal (`s(animal, bs = 're')`),  
199 fixed-effect intercepts for each species (`species`), and species-level by smooths (`s(...,`  
200 `by = species)`), which allowed each species' term to be estimated independent of other  
201 species (see model I in Figure 4 of Pedersen *et al.*, 2019). The `by` smooths accounted for  
202 trends in time of day (in Pacific Daylight Time; `tod_pdt`), day of year (`doy`), and tempera-  
203 ture (`temp_c`). The models also had three tensor product interaction terms (`ti()`) by each  
204 species: (1) day of year and time of day, (2) temperature and time of day, and (3) tempera-  
205 ture and day of year. These three terms accounted for: (1) seasonal changes in day length,  
206 (2) hourly changes in the response to temperature (e.g., changes in nocturnality), and (3)  
207 seasonal changes in the response to temperature (e.g., changes in coats and migration tim-  
208 ing). Finally, smooth terms of log-transformed hours between GPS locations (`dt`) accounted  
209 for irregular sampling rates. A global term of `log(dt)` accounted for the overall effect  
210 of sampling interval, while a factor-smooth interaction term (`s(log(dt), species, bs =`  
211 `'fs')`) allowed for species-level deviations from the global term while assuming a common  
212 smoothness parameter across species (see model GS in Figure 4 of Pedersen *et al.*, 2019).

213 The HGAMs accounted for the cyclicity of time of day and day of year using cyclic  
214 cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). We fit the models with fast Restricted  
215 Maximum Likelihood ('fREML') and discretized covariates (`discrete = TRUE`) to optimize  
216 computational efficiency with no appreciable losses to model performance (Appendix B;  
217 Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma  
218 HGAM inform us on an animal's long-term average speed, since it is the product of the  
219 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)))

```

### 220 2.3.3 Effects of temperature on habitat selection

221 We estimated the effects of temperature on each species' selection for percent forest cover  
 222 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-  
 223 ting a Hierarchical Resource Selection Function for each species using an HGAM with a  
 224 Poisson family of distributions and log link function (Appendix B; Aarts *et al.*, 2008). We  
 225 accounted for the spatiotemporal autocorrelation in the telemetry locations by weighting  
 226 each point based on the telemetry's Autocorrelated Kernel Density Estimate (Fleming &  
 227 Calabrese, 2017; Noonan *et al.*, 2019b) to produce estimates of second- and third-order  
 228 habitat selection (Johnson, 1980). While we recognize there are other important drivers  
 229 of habitat selection (e.g., forest age, forest type, terrain ruggedness, prey availability), we  
 230 decided to only use these three proxies to produce results that are easily comparable across  
 231 species. Each species' model had the same 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)

```

232 Smooth effects of percent forest cover, elevation, and distance to water accounted for  
 233 the species-level average selection strength for each resource. A random effect for each in-  
 234 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
 235 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
 236 selection (i.e., individual-level deviations from the species-level average). Tensor interaction  
 237 product terms (`ti()`) of the three resources and temperature estimated the change in re-  
 238 source selection at different temperatures. Finally, we included marginal smooth terms of  
 239 temperature to account for species- and individual-level sampling biases over temperature  
 240 (e.g., sampling more during warm periods). Detections were weighted proportionally to their  
 241 degree of independence from other temporally proximate detections (`weights = weight` –  
 242 Appendix B; Alston *et al.*, 2022), while quadrature points had a weight of 1. Quadrature  
 243 points were obtained using all raster cells in the 99.9% AKDE percentile. The number of  
 244 quadrature locations greatly outnumbered the number of observed locations (Fig. B11),  
 245 especially after accounting for weighting based on the degree of autocorrelation and the  
 246 number of home range crossings (Fig. B12).

<sup>247</sup> **3 Results**

<sup>248</sup> Overall, 2.6% of GPS locations had temperatures lower than  $-20^{\circ}\text{C}$ , while 6.5% had temper-  
<sup>249</sup> atures above  $20^{\circ}\text{C}$ , and temperature ranges differed across species (Table 2, Fig. B2). At  $0^{\circ}\text{C}$ ,  
<sup>250</sup> species differed in overall mean probabilities of movement (range: 0.05 – 0.31), mean speed  
<sup>251</sup> when moving (range: 0.42 – 2.67 km/h), and mean distance traveled (i.e.,  $P(M) \times \mathbb{E}(S)$ ,  
<sup>252</sup> range: 0.04 – 0.61 km/h; Table 3). Grizzly bears tended to move least often ( $P(M) \approx 0.05$ ),  
<sup>253</sup> while wolves and cougars moved most often ( $P(M) \geq 0.22$ ). When moving, mountain goats  
<sup>254</sup> and southern mountain caribou moved the slowest ( $\mathbb{E}(S|M) \approx 0.43$  km/h), while wolves  
<sup>255</sup> had the highest mean speed when moving ( $\mathbb{E}(S|M) \approx 2.64$  km/h). Consequently, wolves  
<sup>256</sup> 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

257 Near  $0^\circ\text{C}$ , wolves selected for dense forest cover ( $\gtrapprox 50\%$ ), elevations near 1 km, and  
 258 distances from water  $< 10$  km; elk selected for forest cover near 50%, elevations between  
 259 1 and 2 km, and distances from water of 5-15 km; mountain goats selected for sparse (<  
 260 50%) forest cover, elevations between 1 and 2 km; cougars selected for dense forest cover,  
 261 an elevation of  $\sim 1$  km, and distances from water  $< 10$  km; boreal caribou selected for  
 262 intermediate to dense forest cover, elevations near 500 m, and distances from water  $< 10$   
 263 km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and  
 264 distances from water  $< 5$  km; and grizzly bears selected for sparse forest cover (25-50%),  
 265 elevation near 1 km, and distances from water  $< 2$  km.

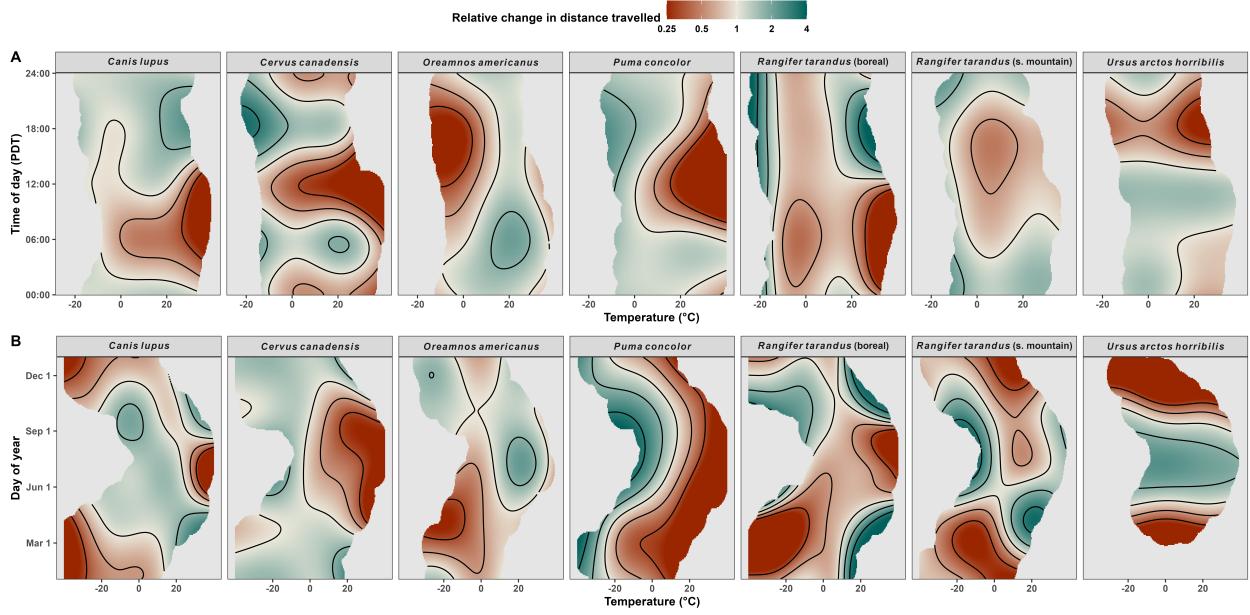
266 There was relatively strong agreement between models with and without temperature  
 267 (Figs. B3, and B13), but including temperature always resulted in better fits. All analyses  
 268 of deviance showed that temperature significantly affected movement behavior (all p-values  
 269  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \geq 342$ ; Appendix B). Accounting for temperature resulted in a  
 270 simpler HRSF for mountain goats (lower model degrees of freedom) that fit the data better  
 271 (lower deviance), and hence no test was necessary to show that the inclusion of temperature  
 272 produced a better fit.

273 **3.1 Effects of temperature on movement rates**

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

291 **3.2 Effects of temperature on habitat selection**

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

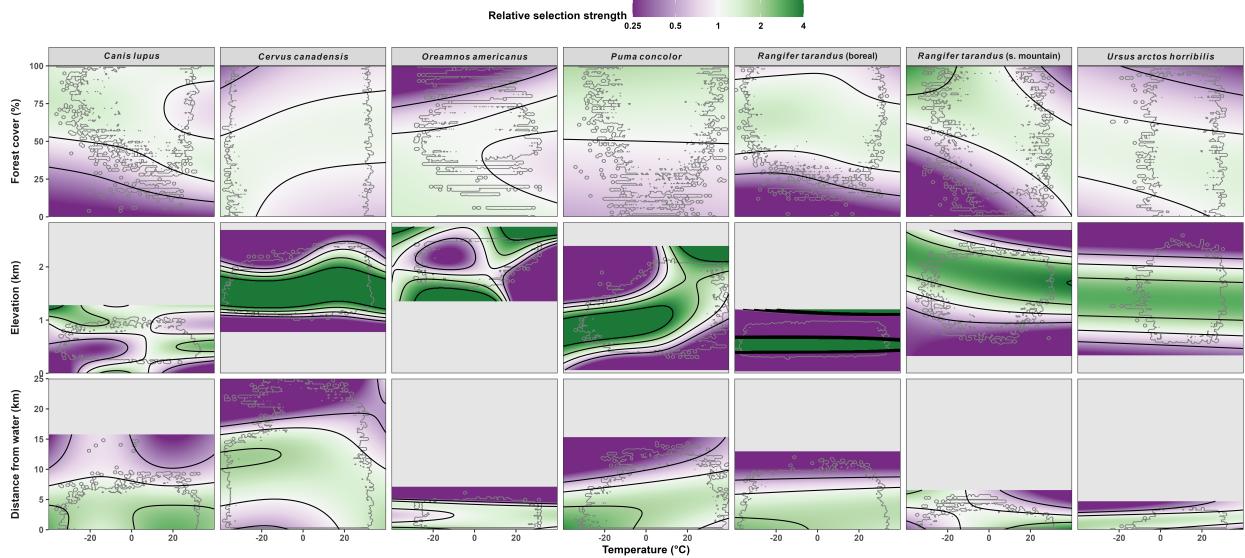


**Figure 3: Temperature is a strong determinant of how far and when mammals travel.** The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1<sup>st</sup> (**A**) and day of year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

299 towards more intermediate forest cover without much of a change in preference width. All  
300 species shifted elevationally with temperature, although boreal caribou's selection strength  
301 for elevation was less sensitive to elevation. Overall, as temperatures rose, elk, mountain  
302 goats, and cougars increased in elevation, while boreal wolves, southern mountain caribou,  
303 and grizzly bears decreased in elevation. Most species generally remained within 5 km of  
304 water, and temperature did not affect their selection strength as much as for the other two  
305 resources. Again, estimated RSS values were generally most uncertain at extreme tempera-  
306 tures (Fig. B14).

### 307 3.3 Predicted changes in movement during the 21<sup>st</sup> century

308 Species varied in both the direction and magnitude of predicted change in distance trav-  
309 eled, but worse climate-change scenarios always corresponded to greater absolute changes  
310 in behaviour (Figs. 5, B9, and B10). Under the best-case scenario, absolute changes by  
311 2100 were small (approximately 0% to 4%), while under the worst-case scenario absolute  
312 changes ranged from ~2% (grizzly bear) to ~25% (cougars). However, while the models esti-



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

313 mated that grizzly bears would move substantially less (if at all) in winter (Figs. 3, B4-B6),  
 314 the models did not explicitly account for changes in hibernation phenology. Consequently,  
 315 the climate change projections do not explicitly account for changes in energetic needs or  
 316 physiology. Throughout BC (Fig. 6), all species showed little to no absolute change under  
 317 the best-case scenario (approximately 0-4% relative to 2025, on average), and approximately  
 318 2-25% average absolute change under the worst-case scenario, but the predicted changes var-  
 319 ied spatially due to heterogeneity in climate change. Again, absolute changes were smallest  
 320 under the best-case scenario and greatest under the worst-case scenario for all species.

321 We do not predict any of the species to exhibit stronger selection for their current range,  
 322 irrespective of climate change scenario. Changes in RSS by 2100 were between 0% and -3%  
 323 under the best-case scenario, but they ranged from -8% to -14% under the worst-case scenario  
 324 (Fig. 7). As with distance traveled, the change in RSS in 2100 varied throughout BC for all  
 325 species (Fig. 8). All species were predicted to exhibit a decrease in RSS throughout most of  
 326 BC, with the exception of boreal caribou, which had a predicted increase in approximately  
 327 67% of the province, including their current range. The increase was in great part due to the  
 328 estimated increase in selection for high-elevation areas that are well outside the population's  
 329 current range.

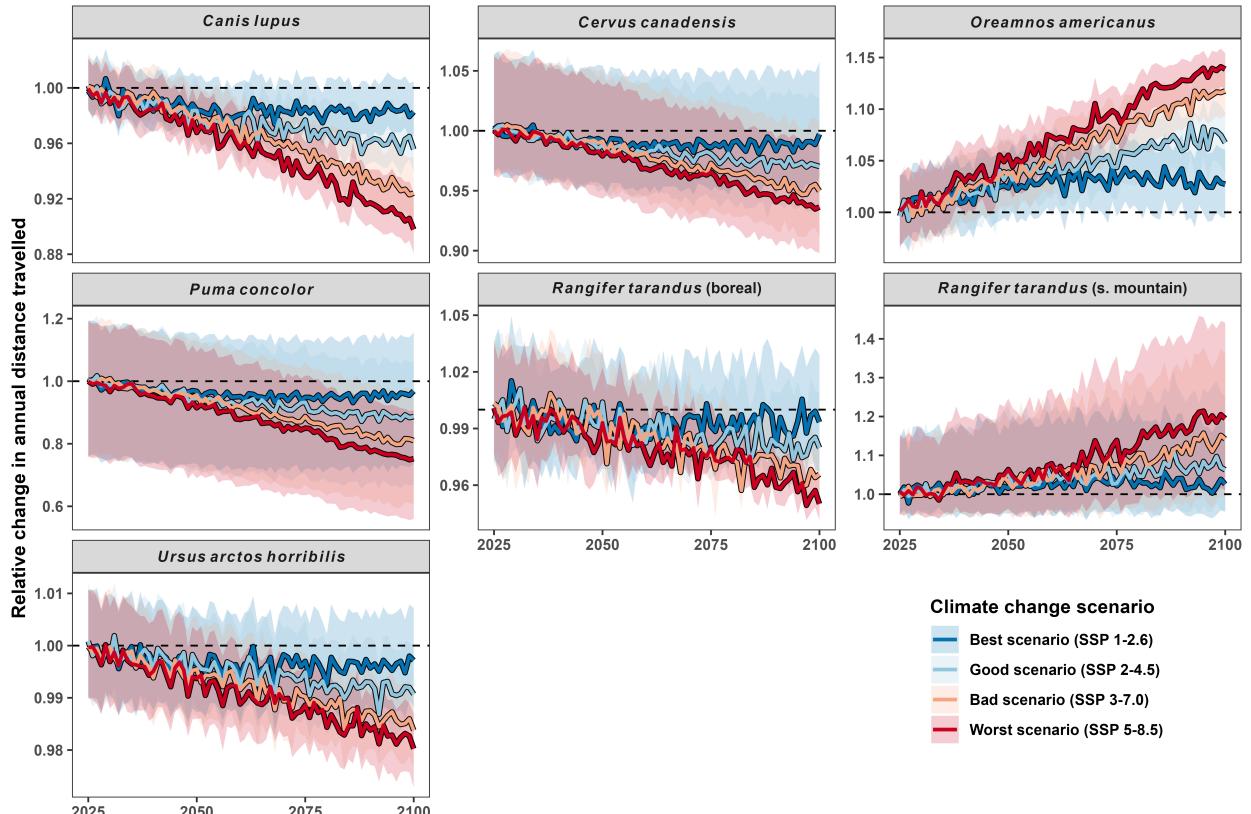
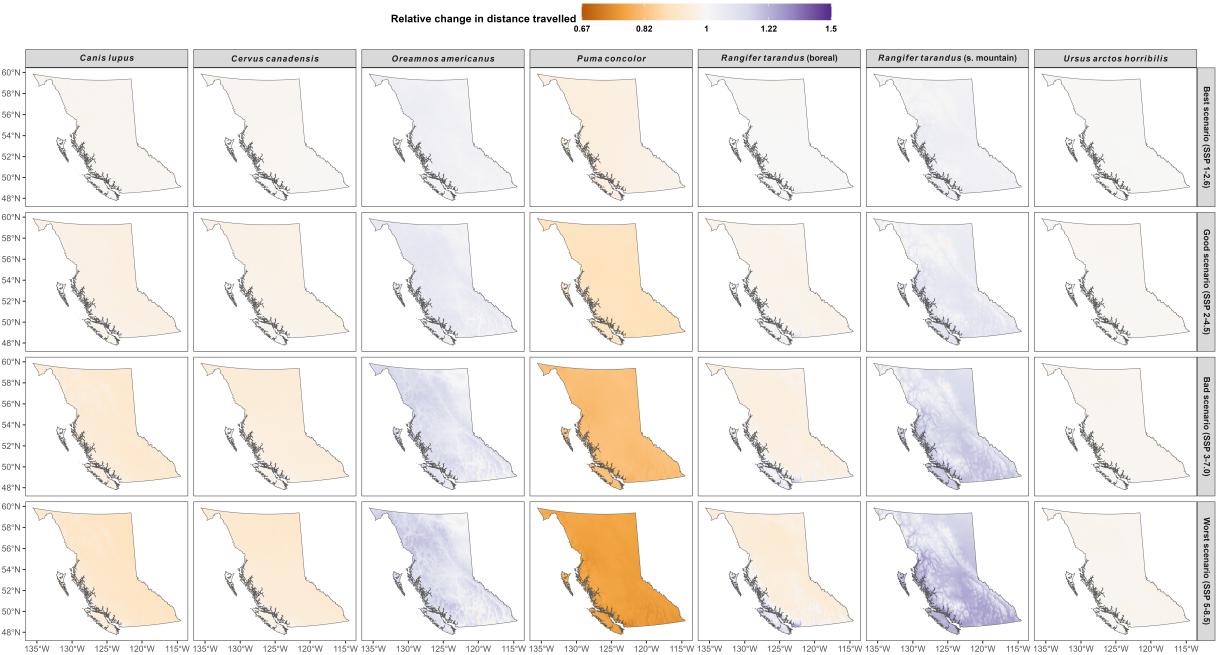


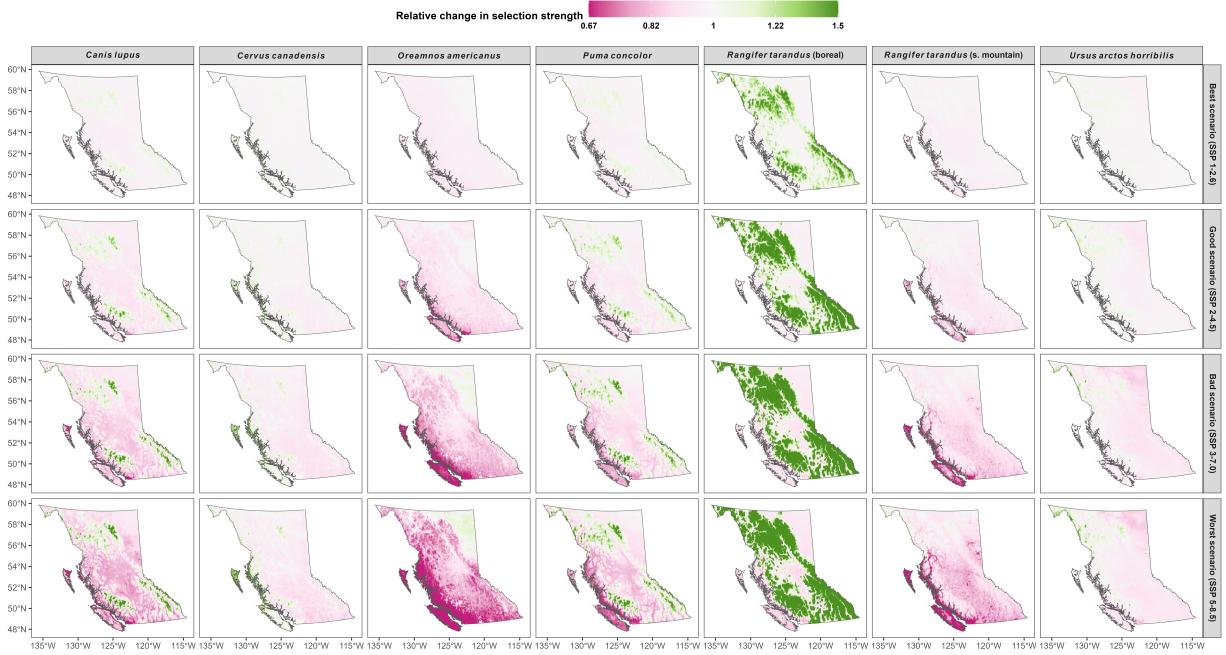
Figure 5: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the 90% prediction interval within the range. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). The projections only account for changes in movement in 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 location's average distance in 2025 across all four scenarios, such that 1 indicates no change, 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 0.72 to 1.29). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest cover.



**Figure 7: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario.** Lines indicate the projected change in RSS for the bottom 5%, median, and top 5% RSS values within the species' current extent. Changes are relative to the mean RSS for each quantile in 2025 across the four Shared Socioeconomic Pathways (SSPs).



**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, such that 1 indicates no change, 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 0.26 to 117). The increase in boreal caribou’s RSS for high elevations at warmer temperatures was highly uncertain and often not credible at the 95% level.

## 330 4 Discussion

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

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

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

350 Changes in animal movement behavior may also alter the frequency and intensity of  
351 human-wildlife conflict, especially with the addition of growing pressures from human de-  
352 velopment and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At  
353 the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*,  
354 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease  
355 (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being  
356 preyed on (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022;  
357 Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009;  
358 Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences  
359 for population and ecosystem structures and dynamics as prey, predators, and competitors  
360 experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et*  
361 *al.*, 2011).

362 Our ability to respond changes in climate is contingent on our ability to prepare for and  
363 predict change. However, predicting animal behaviour becomes increasingly complicated as  
364 the conditions animals are exposed to deviate from current, typical conditions, especially  
365 when responses are nonlinear and data are sparse. Consequently, we do not present our  
366 results as a definitive guide to how mammals in BC will respond to climate change. Instead,  
367 we hope they serve as a starting point to (1) demonstrate that mammals' movement rates and  
368 habitat selection depend on temperature and (2) how one can estimate mammals' changes  
369 in movement behaviour due to climate change. Additionally, communicating uncertainty

<sup>370</sup> in one's estimates is crucial in assessing risk probabilistically, and appropriate measures of  
<sup>371</sup> uncertainty require careful and robust modeling (Aven & Kvaløy, 2002; Ayre & Landis, 2012;  
<sup>372</sup> Czado & Brechmann, 2014).

<sup>373</sup> Recent events in global politics, including global conflicts (McNutt & Hildebrand, 2022;  
<sup>374</sup> Tollefson, 2022) and the rapid rise in generative machine learning (more commonly: “AI,”  
<sup>375</sup> see Roumeliotis & Tselikas, 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*, 2025)  
<sup>376</sup> and its prohibitive energy and water demands (Li *et al.*, 2023) and carbon footprint (Luc-  
<sup>377</sup> cioni *et al.*, 2024), have placed doubt on the feasibility of reaching climate change goals that  
<sup>378</sup> seemed achievable in the past decade (United Nations Environment Programme *et al.*, 2024).

<sup>379</sup> Mitigating climate change and its consequences will require extensive and widespread collab-  
<sup>380</sup> orative effort (Huang & Zhai, 2021). Similarly, protecting a third of the world’s ecosystems  
<sup>381</sup> (Convention on Biological Diversity, 2022) appears less achievable as global political and  
<sup>382</sup> environmental conditions change rapidly and unpredictably (Sih *et al.*, 2011; Simmons *et*  
<sup>383</sup> *al.*, 2021; Guenette *et al.*, 2022; Sovacool *et al.*, 2023). Achieving the “30 by 30” goal will  
<sup>384</sup> require international collaboration as well as active partnership with local Peoples, especially  
<sup>385</sup> Indigenous Peoples (Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences  
<sup>386</sup> of climate change on mammals’ movement behaviour is a first step towards proactively re-  
<sup>387</sup> sponding to how mammals will respond to human-induced rapid environmental change (Sih  
<sup>388</sup> *et al.*, 2011; Williams & Blois, 2018). In the following sections, we discuss the implications  
<sup>389</sup> of our results in more detail. We then expand on consequences for conservation during the  
<sup>390</sup> 21<sup>st</sup> century and considerations for future studies.

#### <sup>391</sup> 4.1 Effects of temperature on movement rates

<sup>392</sup> The heterogeneity mammals’ responses to temperature suggests that ecological communities  
<sup>393</sup> will respond to change in complex and interconnected ways. Although our models do not  
<sup>394</sup> account for explicit physiological or phenological changes, the surfaces in Fig. 3 suggest that  
<sup>395</sup> 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 British Columbia will have community-wide impacts on movement rates, encounter rates, and potentially community structure (Martinez-Garcia *et al.*, 2020). More work is necessary on quantifying interspecific responses to temperature, including the effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et al.*, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021; Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at the current rate of climate change (Hatem *et al.*, 2014; Williams & Blois, 2018), especially since landscape changes will likely depend not only on the direct effect of temperature but also on cascading changes in the availability and unpredictability of resources (McLellan & McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

## 414 4.2 Effects of temperature on habitat selection

415 As with the effects of temperature on movement rates, the heterogeneity of temperature  
416 effects on species' habitat selection indicates that efficient and proactive habitat conservation  
417 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
418 physiological responses to temperature that may impact movement, such as changes in the  
419 phenology of plants, fire, ice, or mammalian physiology (e.g., moulting, fat storages) or  
420 behaviour (e.g., migration, food caching), other than as direct responses to temperature.  
421 Consequently, the behavioural changes we present should be interpreted carefully. While

422 some seasonal cycles do not depend directly on temperature and may thus not be impacted  
423 directly by climate change (such as those driven by photoperiod, see Liu *et al.*, 2022), the  
424 predictions we present also rely on the assumption that mammals will not adapt these  
425 seasonal cycles to temperature-dependent cues, such as weather (Xu & Si, 2019) or forage  
426 availability (Middleton *et al.*, 2018), which may not be correct. Additionally, it is important  
427 to stress the distinction between habitat selection and quality. While animals tend to select  
428 for high-quality habitats (Kacelnik *et al.*, 1992; Wright, 2024), high selection strength can  
429 also be a consequence of an ecological trap (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*,  
430 2021).

### 431 4.3 Predicted changes in movement during the 21<sup>st</sup> century

432 Achieving the goals laid out by the “30 by 30” conservation initiative (Convention on  
433 Biological Diversity, 2022) will require careful planning but often also rapid action. In the  
434 case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the  
435 end of 2023 (Environment and Climate Change Canada, 2024; Minister of Environment  
436 and Climate Change, 2024). Additionally, efficient and effective conservation will require  
437 collaboration with Indigenous and local communities to ensure Treaties are respected in the  
438 process (Turner & Clifton, 2009; Wong *et al.*, 2020; Falardeau *et al.*, 2022; Lamb *et al.*,  
439 2023) while also actively preparing for future change (Desjardins *et al.*, 2020; Hessami *et al.*,  
440 2021).

441 The diversity in predicted changes in movement behavior by 2100 (both across species  
442 and within species’ current ranges) and high spatial heterogeneity in Fig. 8 highlight the  
443 need for careful planning that incorporates not only reliable estimates of change but also  
444 pragmatic and communicable measures of uncertainty and variability around such estimates.  
445 For example, the width of the prediction intervals in Fig. 5 suggest that spatial and intra-  
446 individual variation should be accounted for when deciding the location and size of protected  
447 areas. Population-level means that ignore such variation can greatly limit the efficacy of

448 conservation projects (Muff *et al.*, 2020; Mortlock *et al.*, 2024). Additionally, accurate  
449 estimates of the effects of changes in temperature on mammals' movement require a holistic  
450 view of the direct effects of temperature on mammals' movement directly as well as its effects  
451 on other drivers of movement, such as forage and prey availability (Mezzini *et al.*, 2025),  
452 encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*, 2020), population dynamics (Smith  
453 *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*, 2020), and predation risk (Kohl *et*  
454 *al.*, 2019). This complexity results in the great variation among the responses of different  
455 species (and individuals), especially as populations undergo a rapid cascade of change (Botero  
456 *et al.*, 2015) and animals face increasing pressures from human activity, including habitat  
457 fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009;  
458 Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*,  
459 2024). As selection strength for current ranges changes (and likely decreases), some animals  
460 may disperse, relocate to a new habitat, or remain within the current range despite the  
461 reduced fitness and increased extinction risk (Duncan *et al.*, 2012; Logares & Nuñez, 2012;  
462 Anderson *et al.*, 2017).

#### 463 4.4 Species-specific considerations

##### 464 4.4.1 *Canis lupus*

##### 465 4.4.2 *Cervus canadensis*

##### 466 4.4.3 *Oreamnos americanus*

##### 467 4.4.4 *Puma concolor*

##### 468 4.4.5 *Rangifer tarandus* (boreal)

##### 469 4.4.6 *Rangifer tarandus* (s. mountain)

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

472 (2) crossing the 500 m to > 1,000 m regions is safe and attractive

473 **4.4.7 *Ursus arctos horribilis***

474 **4.5 Considerations for future studies**

475 Our work highlights three central considerations for future research: (1) telemetry sam-  
476 pling rates should be designed primarily in relation to the movement timescales of the species  
477 of interest (Noonan *et al.*, 2019a; Nathan *et al.*, 2022; Pease, 2024), (2) the number of indi-  
478 viduals tracked and the length of each telemetry should depend not just on population size  
479 but also the rate of environmental change, and (3) predicting changes in movement behaviour  
480 becomes highly complex when responses are nonlinear, especially when changes depend on  
481 many interacting factors (Polazzo *et al.*, 2024) and one is interested in predicting responses  
482 in extreme conditions for which data are scarce (Steixner-Kumar & Gläscher, 2020).

483 While the `ctmm` movement models produced scale-independent estimates of speed (i.e.,  
484 model interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accu-  
485 racy, size, and stability of speed estimates still depended on the GPS sampling frequency.  
486 This dependency is because coarsely-sampled movement data contains information on large-  
487 scale movements (range crossings, migrations) but not fine-scale movements, including first-  
488 order habitat selection (Johnson, 1980). Using the boreal caribou as an example, the 13-hour  
489 sampling interval allows us to reasonably estimate the caribou's movement path at a tempo-  
490 ral scale of approximately 13 hours (or greater), but we cannot produce reasonable movement  
491 trajectories at a much finer (e.g., hourly) scale. Nathan *et al.* (2022) provides additional  
492 examples of how the frequency of location data affects the results that can be inferred by  
493 modeling movement behavior. Consequently, we suggest being cautious when comparing esti-  
494 mated movement behaviours across species, even though all predictions have been corrected  
495 to the hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Ide-  
496 ally, sampling schedules should be fine enough to reconstruct animals' movement movement  
497 paths. Good estimates of an animal's speed and trajectory require telemetry locations to

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

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

519 Temperature affects many aspects of mammalian physiology and behavior, including en-  
520 ergetics, sleep, and movement behavior. Climatic changes during the last two centuries have  
521 exposed many mammals to novel and increasingly extreme environmental conditions that  
522 have led to visible changes that impact not only individuals but also ecological and human  
523 communities. However, quantifying the effects of climate change is often complex, espe-  
524 cially as conditions become increasingly different and extreme events become increasingly

common. Accurately quantifying the nonlinear effects of temperature on when, how, and where mammals move requires careful data collection and model design. We have presented a multi-species analysis of the effects of temperature on mammalian movement rates and habitat selection in hopes that other researchers can leverage this framework and models to expand our understanding of how temperature affects the movement behavior of other species, including smaller mammals, more elusive species, and non-mammal animals. Understanding 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.

## 543 5 Author contributions

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

549 **References**

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

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

- 602 300–307.
- 603 Czado C, Brechmann EC (2014) [Bayesian Risk Analysis](#). In: *Risk - A Multidisciplinary*  
604 *Introduction* (eds Klüppelberg C, Straub D, Welpe IM), pp. 207–240. Springer Interna-  
605 tional Publishing, Cham.
- 606 Deb JC, Forbes G, MacLean DA (2020) [Modelling the spatial distribution of selected North](#)  
607 [American woodland mammals under future climate scenarios](#). *Mammal Review*, **50**,  
608 440–452.
- 609 DeepSeek-AI, Guo D, Yang D et al. (2025) [DeepSeek-R1: Incentivizing Reasoning Capability](#)  
610 [in LLMs via Reinforcement Learning](#).
- 611 Desjardins SPA, Friesen TM, Jordan PD (2020) [Looking back while moving forward: How](#)  
612 [past responses to climate change can inform future adaptation and mitigation strategies](#)  
613 [in the Arctic](#). *Quaternary International*, **549**, 239–248.
- 614 Dierauer JR, Allen DM, Whitfield PH (2021) [Climate change impacts on snow and stream-](#)  
615 [flow drought regimes in four ecoregions of British Columbia](#). *Canadian Water Resources*  
616 *Journal / Revue canadienne des ressources hydriques*, **46**, 168–193.
- 617 Duncan C, Chauvenet ALM, McRae LM, Pettorelli N (2012) [Predicting the Future Impact](#)  
618 [of Droughts on Ungulate Populations in Arid and Semi-Arid Environments](#) (ed Seebacher  
619 F). *PLoS ONE*, **7**, e51490.
- 620 Dupont L, Thierry M, Zinger L, Legrand D, Jacob S (2024) [Beyond reaction norms: The](#)  
621 [temporal dynamics of phenotypic plasticity](#). *Trends in Ecology & Evolution*, **39**, 41–51.
- 622 Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR (2023) [The travel speeds of large animals](#)  
623 [are limited by their heat-dissipation capacities](#) (ed Hedenström A). *PLOS Biology*, **21**,  
624 e3001820.
- 625 Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, Windels  
626 SK (2017) [Implications of the thermal environment for terrestrial wildlife management](#).  
627 *Wildlife Society Bulletin*, **41**, 183–193.
- 628 Environment and Climate Change Canada (2024) [Canadian Environmental Sustainability](#)

- 629 Indicators: Canada's conserved areas.
- 630 Falardeau M, Bennett EM, Else B et al. (2022) Biophysical indicators and Indigenous and  
631 Local Knowledge reveal climatic and ecological shifts with implications for Arctic Char  
632 fisheries. *Global Environmental Change*, **74**, 102469.
- 633 Fjelldal MA, Wright J, Stawski C (2021) Nightly torpor use in response to weather conditions  
634 and individual state in an insectivorous bat. *Oecologia*, **197**, 129–142.
- 635 Fleming CH, Calabrese JM (2017) A new kernel density estimator for accurate home-range  
636 and species-range area estimation (ed Dray S). *Methods in Ecology and Evolution*, **8**,  
637 571–579.
- 638 Fleming CH, Calabrese JM (2023) Ctmm: Continuous-Time Movement Modeling.
- 639 Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF (2014) From  
640 Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement  
641 Modes across Spatiotemporal Scales. *The American Naturalist*, **183**, E154–E167.
- 642 Fuller A, Mitchell D, Maloney SK, Hetem RS (2016) Towards a mechanistic understanding  
643 of the responses of large terrestrial mammals to heat and aridity associated with climate  
644 change. *Climate Change Responses*, **3**, 10.
- 645 Gilbert SL, Hundertmark KJ, Person DK, Lindberg MS, Boyce MS (2017) Behavioral plasticity  
646 in a variable environment: Snow depth and habitat interactions drive deer movement  
647 in winter. *Journal of Mammalogy*, **98**, 246–259.
- 648 Giroux A, Ortega Z, Attias N, Desbiez ALJ, Valle D, Börger L, Rodrigues Oliveira-Santos  
649 LG (2023) Activity modulation and selection for forests help giant anteaters to cope with  
650 temperature changes. *Animal Behaviour*, **201**, 191–209.
- 651 Glass TW, Breed GA, Robards MD, Williams CT, Kielland K (2021) Trade-off between pre-  
652 dation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted  
653 mesocarnivore. *Animal Behaviour*, **175**, 163–174.
- 654 Guenette JD, Kenworthy PG, Wheeler CM (2022) Implications of the War in Ukraine for  
655 the Global Economy.<http://documents.worldbank.org/curated/en/099616504292238906>.

- 656 World Bank Group, Washington, D.C.
- 657 Gulland FMD, Baker JD, Howe M et al. (2022) A review of climate change effects on marine  
658 mammals in United States waters: Past predictions, observed impacts, current research  
659 and conservation imperatives. *Climate Change Ecology*, **3**, 100054.
- 660 Hall LE, Chalfoun AD, Beever EA, Loosen AE (2016) Microrefuges and the occurrence of  
661 thermal specialists: Implications for wildlife persistence amidst changing temperatures.  
662 *Climate Change Responses*, **3**, 8.
- 663 Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM (2014) Fine-  
664 grain modeling of species' response to climate change: Holdouts, stepping-stones, and  
665 microrefugia. *Trends in Ecology & Evolution*, **29**, 390–397.
- 666 Hegel TM, Mysterud A, Huettmann F, Stenseth NC (2010) Interacting effect of wolves and  
667 climate on recruitment in a northern mountain caribou population. *Oikos*, **119**, 1453–  
668 1461.
- 669 Hersbach H, Bell B, Berrisford P et al. (2023) ERA5 hourly data on single levels from 1940  
670 to present.
- 671 Hessami MA, Bowles E, Popp JN, Ford AT (2021) Indigenizing the North American Model  
672 of Wildlife Conservation (ed Beazley K). *FACETS*, **6**, 1285–1306.
- 673 Hetem RS, Fuller A, Maloney SK, Mitchell D (2014) Responses of large mammals to climate  
674 change. *Temperature*, **1**, 115–127.
- 675 Hijmans RJ (2023) Terra: Spatial Data Analysis.
- 676 Hollister J, Shah T, Nowosad J, Robitaille AL, Beck MW, Johnson M (2023) Elevatr: Access  
677 Elevation Data from Various APIs.
- 678 Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D (2020) Cold and hungry:  
679 Combined effects of low temperature and resource scarcity on an edge-of-range temperate  
680 primate, the golden snub-nose monkey. *Ecography*, **43**, 1672–1682.
- 681 Huang M-T, Zhai P-M (2021) Achieving Paris Agreement temperature goals requires carbon  
682 neutrality by middle century with far-reaching transitions in the whole society. *Advances*

- 683       in *Climate Change Research*, **12**, 281–286.
- 684   IPCC (2023) *Climate Change 2021 – The Physical Science Basis: Working Group I Con-*  
685       *tribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate*  
686       *Change*, 1st edn. Cambridge University Press.
- 687   Jahn M, Seebacher F (2022) *Variations in cost of transport and their ecological consequences:*  
688       *A review*. *Journal of Experimental Biology*, **225**, jeb243646.
- 689   Johnson DH (1980) *The Comparison of Usage and Availability Measurements for Evaluating*  
690       *Resource Preference*. *Ecology*, **61**, 65–71.
- 691   Johnson HE, Lewis DL, Verzuh TL, Wallace CF, Much RM, Willmarth LK, Breck SW (2018)  
692       *Human development and climate affect hibernation in a large carnivore with implications*  
693       *for human–carnivore conflicts* (ed Bieber C). *Journal of Applied Ecology*, **55**, 663–672.
- 694   Kacelnik A, Krebs JR, Bernstein C (1992) *The ideal free distribution and predator-prey*  
695       *populations*. *Trends in Ecology & Evolution*, **7**, 50–55.
- 696   Kays R, Davidson SC, Berger M et al. (2022) *The Movebank system for studying global*  
697       *animal movement and demography*. *Methods in Ecology and Evolution*, **13**, 419–431.
- 698   Kohl MT, Ruth TK, Metz MC, Stahler DR, Smith DW, White PJ, MacNulty DR (2019) *Do*  
699       *prey select for vacant hunting domains to minimize a multi-predator threat?* (ed Gaillard  
700       J). *Ecology Letters*, **22**, 1724–1733.
- 701   Lamb CT, Willson R, Menzies AK et al. (2023) *Braiding Indigenous rights and endangered*  
702       *species law*. *Science*, **380**, 694–696.
- 703   Leclerc M, Leblond M, Le Corre M, Dussault C, Côté SD (2021) *Determinants of migra-*  
704       *tion trajectory and movement rate in a long-distance terrestrial mammal* (ed Reyna R).  
705       *Journal of Mammalogy*, **102**, 1342–1352.
- 706   Levins RA (1974) *Evolution in changing environments: Some theoretical explorations*, 3.  
707       printing edn. Princeton Univ. Press, Princeton, NJ.
- 708   Li Z, Wood SN (2020) *Faster model matrix crossproducts for large generalized linear models*  
709       *with discretized covariates*. *Statistics and Computing*, **30**, 19–25.

- 710 Li P, Yang J, Islam MA, Ren S (2023) [Making AI Less "Thirsty": Uncovering and Addressing](#)  
711 [the Secret Water Footprint of AI Models.](#)
- 712 Liu JA, Meléndez-Fernández OH, Bumgarner JR, Nelson RJ (2022) [Effects of light pollution](#)  
713 [on photoperiod-driven seasonality. \*Hormones and Behavior\*, \*\*141\*\*, 105150.](#)
- 714 Logares R, Nuñez M (2012) [Black Swans in ecology and evolution: The importance of](#)  
715 [improbable but highly influential events. \*Ideas in Ecology and Evolution\*.](#)
- 716 Luccioni AS, Viguier S, Ligozat A-L (2024) Estimating the carbon footprint of BLOOM, a  
717 176B parameter language model. *J. Mach. Learn. Res.*, **24**.
- 718 Malpeli KC (2022) [Ungulate migration in a changing climate—An initial assessment of cli-](#)  
719 [mate impacts, management priorities, and science needs. Reston, VA.](#)
- 720 Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM (2020) [How range res-](#)  
721 [idency and long-range perception change encounter rates. \*Journal of Theoretical Biology\*,](#)  
722 [\*\*498\*\*, 110267.](#)
- 723 Matthiopoulos J (2022) [Defining, estimating, and understanding the fundamental niches of](#)  
724 [complex animals in heterogeneous environments. \*Ecological Monographs\*, \*\*92\*\*, e1545.](#)
- 725 McCain CM (2019) [Assessing the risks to United States and Canadian mammals caused](#)  
726 [by climate change using a trait-mediated model \(ed Heske E\). \*Journal of Mammalogy\*,](#)  
727 [\*\*gyz155.\*\*](#)
- 728 McElreath R (2020) [Statistical rethinking: A Bayesian course with examples in R and Stan,](#)  
729 [Second edition edn. CRC Press, Boca Raton London New York.](#)
- 730 McLellan ML, McLellan BN (2015) [Effect of Season and High Ambient Temperature on](#)  
731 [Activity Levels and Patterns of Grizzly Bears \(\*Ursus arctos\*\) \(ed Crocker DE\). \*PLOS\*](#)  
732 [\*\*ONE\*\*, \*\*10\*\*, e0117734.](#)
- 733 McNab BK (1970) [Body Weight and the Energetics of Temperature Regulation. \*Journal of\*](#)  
734 [\*Experimental Biology\*, \*\*53\*\*, 329–348.](#)
- 735 McNutt M, Hildebrand J (2022) [Scientists in the line of fire. \*Science\*, \*\*375\*\*, 1071–1071.](#)
- 736 Melin M, Matala J, Mehtätalo L, Pusenius J, Packalen T (2023) [The effect of snow depth](#)

- 737       on movement rates of GPS-collared moose. *European Journal of Wildlife Research*, **69**,  
738       21.
- 739       Merkle JA, Monteith KL, Aikens EO et al. (2016) Large herbivores surf waves of green-up  
740       during spring. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160456.
- 741       Mezzini S, Fleming CH, Medici EP, Noonan MJ (2025) How resource abundance and resource  
742       stochasticity affect organisms' range sizes. *Movement Ecology*, **13**, 20.
- 743       Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, Kauffman MJ  
744       (2018) Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, **127**, 1060–  
745       1068.
- 746       Minister of Environment and Climate Change (2024) An Act respecting transparency and ac-  
747       countability in relation to certain commitments Canada has made under the Convention  
748       on Biological Diversity.
- 749       Montgomery RA, Redilla KM, Moll RJ, Van Moorter B, Rolandsen CM, Millspaugh JJ,  
750       Solberg EJ (2019) Movement modeling reveals the complex nature of the response of  
751       moose to ambient temperatures during summer. *Journal of Mammalogy*, **100**, 169–177.
- 752       Morley ID (2021) Spatiotemporal analysis of ecosystem change and landscape connectivity  
753       using satellite imagery in west-central British Columbia, Canada.
- 754       Mortlock E, Silovsky V, Güldenpfennig J et al. (2024) Sleep in the wild: The importance  
755       of individual effects and environmental conditions on sleep behaviour in wild boar. *Pro-  
756       ceedings of the Royal Society B: Biological Sciences*, **291**, 20232115.
- 757       Mota-Rojas D, Titto CG, Orihuela A et al. (2021) Physiological and Behavioral Mechanisms  
758       of Thermoregulation in Mammals. *Animals*, **11**, 1733.
- 759       Muff S, Signer J, Fieberg J (2020) Accounting for individual-specific variation in habi-  
760       tat-selection studies: Efficient estimation of mixed-effects models using Bayesian or fre-  
761       quentist computation (ed Wal EV). *Journal of Animal Ecology*, **89**, 80–92.
- 762       Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A  
763       movement ecology paradigm for unifying organismal movement research. *Proceedings of*

- 764       *the National Academy of Sciences*, **105**, 19052–19059.
- 765   Nathan R, Monk CT, Arlinghaus R et al. (2022) Big-data approaches lead to an increased  
766       understanding of the ecology of animal movement. *Science*, **375**, eabg1780.
- 767   Noonan MJ, Tucker MA, Fleming CH et al. (2019b) A comprehensive analysis of autocor-  
768       relation and bias in home range estimation. *Ecological Monographs*, **89**, e01344.
- 769   Noonan MJ, Fleming CH, Akre TS et al. (2019a) Scale-insensitive estimation of speed and  
770       distance traveled from animal tracking data. *Movement Ecology*, **7**, 35.
- 771   Pease BS (2024) Ecological scales of effect vary across space and time. *Ecography*, **2024**,  
772       e07163.
- 773   Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models  
774       in ecology: An introduction with mgcv. *PeerJ*, **7**, e6876.
- 775   Pedersen SH, Bentzen TW, Reinking AK et al. (2021) Quantifying effects of snow depth on  
776       caribou winter range selection and movement in Arctic Alaska. *Movement Ecology*, **9**,  
777       48.
- 778   Peterson AN, Soto AP, McHenry MJ (2021) Pursuit and Evasion Strategies in the Predator–  
779       Prey Interactions of Fishes. *Integrative and Comparative Biology*, **61**, 668–680.
- 780   Pigeon KE, Stenhouse G, Côté SD (2016) Drivers of hibernation: Linking food and weather  
781       to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology*, **70**, 1745–  
782       1754.
- 783   Polazzo F, Limberger R, Pennekamp F, Ross SRP-J, Simpson GL, Petchey OL (2024) Mea-  
784       suring the Response Diversity of Ecological Communities Experiencing Multifarious En-  
785       vironmental Change. *Global Change Biology*, **30**, e17594.
- 786   R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foun-  
787       dation for Statistical Computing, Vienna, Austria.
- 788   Riahi K, Vuuren DP van, Kriegler E et al. (2017) The Shared Socioeconomic Pathways and  
789       their energy, land use, and greenhouse gas emissions implications: An overview. *Global*  
790       *Environmental Change*, **42**, 153–168.

- 791 Rice WL (2022) **The conspicuous consumption of wilderness, or leisure lost in the wilderness.**
- 792     *World Leisure Journal*, **64**, 451–468.
- 793 Rigby RA, Stasinopoulos DM (2005) **Generalized additive models for location, scale and**
- 794     **shape (with discussion)**. *Journal of the Royal Statistical Society: Series C (Applied*
- 795     *Statistics)*, **54**, 507–554.
- 796 Rosenthal J, Booth R, Carolan N et al. (2022) **The impact of recreational activities on**
- 797     **species at risk in Canada**. *Journal of Outdoor Recreation and Tourism*, **40**, 100567.
- 798 Roumeliotis KI, Tselikas ND (2023) **ChatGPT and Open-AI Models: A Preliminary Review**.
- 799     *Future Internet*, **15**, 192.
- 800 Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009) **Identifying and prioritizing ungulate**
- 801     **migration routes for landscape-level conservation**. *Ecological Applications*, **19**, 2016–2025.
- 802 Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL (2019) **Migratory plastic-**
- 803     **ity is not ubiquitous among large herbivores** (ed Chapman J). *Journal of Animal Ecology*,
- 804     **88**, 450–460.
- 805 Schmidt NM, Grøndahl C, Evans AL et al. (2020) **On the interplay between hypothermia**
- 806     **and reproduction in a high arctic ungulate**. *Scientific Reports*, **10**, 1514.
- 807 Sherwood SC, Huber M (2010) **An adaptability limit to climate change due to heat stress**.
- 808     *Proceedings of the National Academy of Sciences*, **107**, 9552–9555.
- 809 Sih A, Ferrari MCO, Harris DJ (2011) **Evolution and behavioural responses to human-**
- 810     **induced rapid environmental change: Behaviour and evolution**. *Evolutionary Applica-*
- 811     *tions*, **4**, 367–387.
- 812 Simmons BA, Nolte C, McGowan J (2021) **Tough questions for the “30 × 30” conservation**
- 813     **agenda**. *Frontiers in Ecology and the Environment*, **19**, 322–323.
- 814 Slatyer RA, Umbers KDL, Arnold PA (2022) **Ecological responses to variation in seasonal**
- 815     **snow cover**. *Conservation Biology*, **36**, e13727.
- 816 Smith BJ, MacNulty DR, Stahler DR, Smith DW, Avgar T (2023) **Density-dependent habitat**
- 817     **selection alters drivers of population distribution in northern Yellowstone elk**. *Ecology*

- 818        *Letters*, **26**, 245–256.
- 819    Sovacool BK, Baum C, Low S (2023) The next climate war? Statecraft, security, and  
820        weaponization in the geopolitics of a low-carbon future. *Energy Strategy Reviews*, **45**,  
821        101031.
- 822    Stasinopoulos MD, Rigby RA (2007) Generalized additive models for location scale and  
823        shape (GAMLSS) in R. *Journal of Statistical Software*, **23**.
- 824    Steixner-Kumar S, Gläscher J (2020) Strategies for navigating a dynamic world. *Science*,  
825        **369**, 1056–1057.
- 826    Sullender BK, Cunningham CX, Lundquist JD, Prugh LR (2023) Defining the danger zone:  
827        Critical snow properties for predator–prey interactions. *Oikos*, **2023**, e09925.
- 828    Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R (2021) An overview of  
829        ecological traps in marine ecosystems. *Frontiers in Ecology and the Environment*, **19**,  
830        234–242.
- 831    Tan M, Zhang S, Stevens M, Li D, Tan EJ (2024) Antipredator defences in motion: Animals  
832        reduce predation risks by concealing or misleading motion signals. *Biological Reviews*,  
833        **99**, 778–796.
- 834    Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial loco-  
835        motion. I. Metabolic energy consumption as a function of speed and body size in birds  
836        and mammals. *Journal of Experimental Biology*, **97**, 1–21.
- 837    Tollefson J (2022) What the war in Ukraine means for energy, climate and food. *Nature*,  
838        **604**, 232–233.
- 839    Tórrez-Herrera LL, Davis GH, Crofoot MC (2020) Do Monkeys Avoid Areas of Home Range  
840        Overlap Because They Are Dangerous? A Test of the Risk Hypothesis in White-Faced  
841        Capuchin Monkeys (*Cebus capucinus*). *International Journal of Primatology*, **41**, 246–  
842        264.
- 843    Tuanmu M, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and  
844        ecosystem modelling. *Global Ecology and Biogeography*, **23**, 1031–1045.

- 845 Tucker MA, Böhning-Gaese K, Fagan WF et al. (2018) **Moving in the Anthropocene: Global**  
846 **reductions in terrestrial mammalian movements.** *Science*, **359**, 466–469.
- 847 Turner NJ, Clifton H (2009) “It’s so different today”: Climate change and indigenous lifeways  
848 in British Columbia, Canada. *Global Environmental Change*, **19**, 180–190.
- 849 Tysor CS (2025) Countergradient variation in lodgepole pine flowering phenology.
- 850 United Nations Environment Programme, Olhoff A, Bataille C et al. (2024) **Emissions Gap**  
851 **Report 2024: No more hot air ... please! With a massive gap between rhetoric and reality,**  
852 **countries draft new climate commitments.** United Nations Environment Programme.
- 853 Van Noorden R, Webb R (2023) ChatGPT and science: The AI system was a force in 2023  
854 — for good and bad. *Nature*, **624**, 509–509.
- 855 Verzuh TL, Rogers SA, Mathewson PD et al. (2023) Behavioural responses of a large,  
856 heat-sensitive mammal to climatic variation at multiple spatial scales. *Journal of Animal*  
857 *Ecology*, **92**, 619–634.
- 858 Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM (2022) Life history consequences of  
859 **climate change in hibernating mammals: A review.** *Ecography*, **2022**, e06056.
- 860 Weststrate DK, Chhen A, Mezzini S, Safford K, Noonan MJ (2024) How climate change  
861 and population growth will shape attendance and human-wildlife interactions at British  
862 Columbia parks. *Journal of Sustainable Tourism*, 1–15.
- 863 Williams JE, Blois JL (2018) Range shifts in response to past and future climate change:  
864 Can climate velocities and species’ dispersal capabilities explain variation in mammalian  
865 range shifts? *Journal of Biogeography*, **45**, 2175–2189.
- 866 Wilson RS, Franklin CE, Davison W, Kraft P (2001) Stenotherms at sub-zero temperatures:  
867 Thermal dependence of swimming performance in Antarctic fish. *Journal of Comparative*  
868 *Physiology B: Biochemical, Systemic, and Environmental Physiology*, **171**, 263–269.
- 869 Winter VA, Smith BJ, Berger DJ et al. (2024) Forecasting animal distribution through in-  
870 dividual habitat selection: Insights for population inference and transferable predictions.  
871 *Ecography*, e07225.

- 872 Wong C, Ballegooien K, Ignace L, Johnson MJ(Gùdia), Swanson H (2020) [Towards rec-](#)  
873 [onciliation: 10 Calls to Action to natural scientists working in Canada](#) (ed Boran I).  
874 *FACETS*, **5**, 769–783.
- 875 Wood SN (2017) Generalized additive models: An introduction with R, Second edition edn.  
876 CRC Press/Taylor & Francis Group, Boca Raton.
- 877 Wood SN, Goude Y, Shaw S (2015) [Generalized additive models for large data sets](#). *Journal*  
878 *of the Royal Statistical Society: Series C (Applied Statistics)*, **64**, 139–155.
- 879 Wood SN, Li Z, Shaddick G, Augustin NH (2017) [Generalized Additive Models for Gigadata:](#)  
880 [Modeling the U.K. Black Smoke Network Daily Data](#). *Journal of the American Statistical*  
881 *Association*, **112**, 1199–1210.
- 882 Woo-Durand C, Matte J-M, Cuddihy G, McGourdji CL, Venter O, Grant JWA (2020) [In-](#)  
883 [creasing importance of climate change and other threats to at-risk species in Canada](#).  
884 *Environmental Reviews*, **28**, 449–456.
- 885 Wright CA (2024) [Survival and movements of mule deer \(\*Odocoileus hemionus\*\) in southern](#)  
886 [British Columbia](#). {PhD} {Thesis}, University of British Columbia.
- 887 Xu F, Si Y (2019) [The frost wave hypothesis: How the environment drives autumn departure](#)  
888 [of migratory waterfowl](#). *Ecological Indicators*, **101**, 1018–1025.
- 889 Xu W, Barker K, Shawler A et al. (2021) [The plasticity of ungulate migration in a changing](#)  
890 [world](#). *Ecology*, **102**, e03293.
- 891 Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, Chen X (2022) [Emergence of](#)  
892 [universal scaling in weather extreme events](#).
- 893 Zhang X, Zhou T, Zhang W et al. (2023) [Increased impact of heat domes on 2021-like heat](#)  
894 [extremes in North America under global warming](#). *Nature Communications*, **14**, 1690.
- 895 Zuñiga-Palacios J, Zuria I, Castellanos I, Lara C, Sánchez-Rojas G (2021) [What do we know](#)  
896 [\(and need to know\) about the role of urban habitats as ecological traps? Systematic](#)  
897 [review and meta-analysis](#). *Science of The Total Environment*, **780**, 146559.
- 898 Zurowski M (2023) The summer Canada burned: The wildfire season that shocked the world.

