

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

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## 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 and where mammals will move 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 not be interpreted individually 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 while calling for a more holistic and collaborative framework.

## <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 al.*,  
59 2023), including forest fires (Zurowski, 2023). As we approach the deadline for the “30 by  
60 30” conservation initiative, a global effort to conserve 30% of the world’s lands and oceans  
61 by 2030 (Section H, Targets 2 and 3 of Convention on Biological Diversity, 2022), decision  
62 makers must understand which areas will be of greatest value for maximizing the project’s  
63 effectiveness. Predicting how climate change will affect how, when, and where animals will  
64 move is necessary for identifying landscape dynamics and value will evolve throughout the  
65 century. Failing to understand how changes in temperature will affect mammalian movement  
66 behaviour and habitat selection will hinder our ability to respond to the current climate crisis  
67 and make 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.

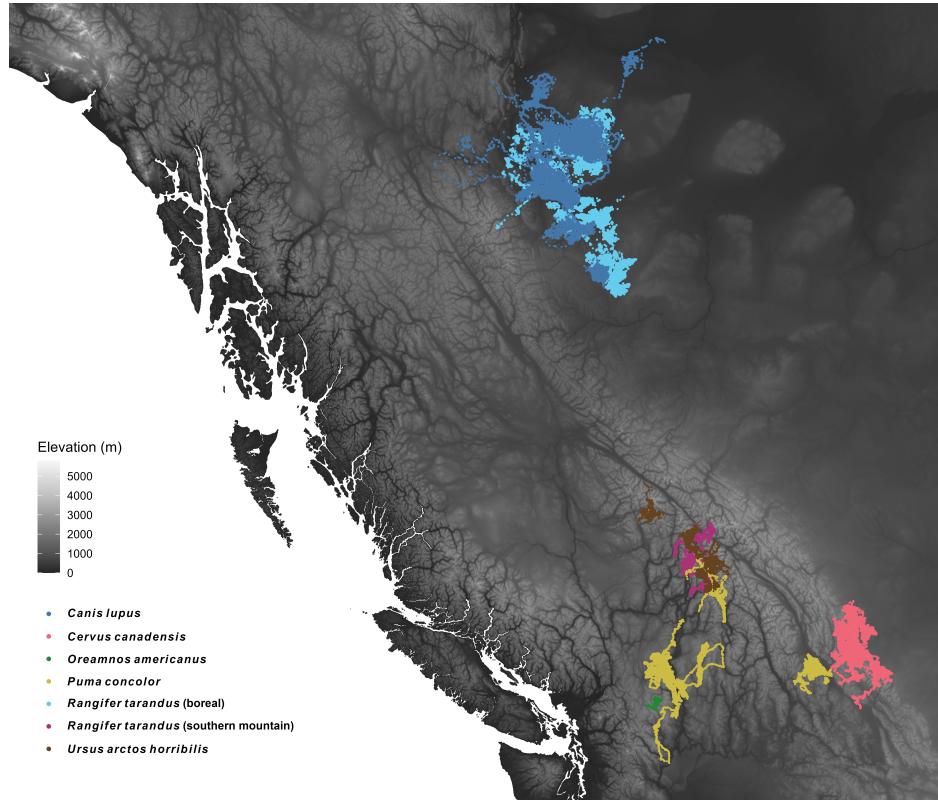


Figure 1: GPS telemetry data for the six species in this study (dots) over a digital elevation model for the study area.

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.

<sup>131</sup> **2.1.3 Resource rasters**

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

<sup>144</sup> **2.2 Estimating mammals' instantaneous speeds**

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

<sup>152</sup> Since 'ctmm's movement models assume stochastic but non-zero speeds (i.e., a sin-  
<sup>153</sup> gle, stochastic moving state), data-informed speeds needed to be corrected so that the  
<sup>154</sup> minimum instantaneous speed could be 0. We performed this correction by subtracting  
<sup>155</sup> each model's mean speed while assuming speeds were  $\chi^2$ -distributed. The function we  
<sup>156</sup> 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. B3).

## 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. We provide the relevant Directed Acyclical Graphs in the  
168 Appendix (Figs. B1-B2).

### 169 **2.3.1 Disentangling direct and indirect effects**

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

181 Indirect effects of temperature also include all effects that can be controlled by altering

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

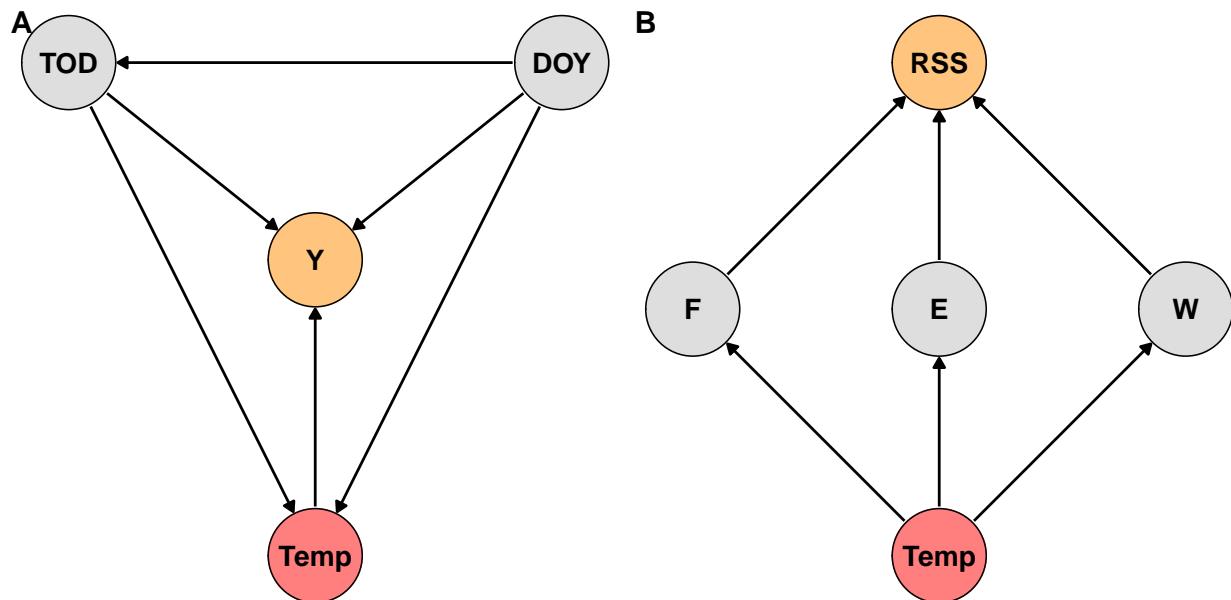


Figure 2: Directed Acyclical Graphs (DAGs) assumed for inferring the causal effects of temperature (Temp) on movement behavior. (A) DAG for the probability of moving, speed when moving, or distance traveled (Y) while accounting for the effects of time of day (TOD), day of year (DOY), and their interaction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

### 190 2.3.2 Effects of temperature on movement rates

191 We estimated the effects of temperature (°C) on mammals' instantaneous movement state  
 192 (moving or not) and speed when moving using two Hierarchical Generalized Additive Models  
 193 (HGAMs, see Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R  
 194 (version 1.9-1, Wood, 2017). The first HGAM estimated the probability that an animal was

195 moving,  $P(M)$ , with a binomial family of distributions and logit link function. The response  
196 variable `moving` was coded as 1 if moving and 0 if not. The second HGAM estimated an  
197 animal's speed when moving (`speed`) with a gamma family of distributions and log link  
198 function.

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

214 The HGAMs accounted for the cyclicity of time of day and day of year using cyclic  
215 cubic splines (`bs = 'cc'`, see p. 202 of Wood, 2017). We fit the models with fast Restricted  
216 Maximum Likelihood ('fREML') and discretized covariates (`discrete = TRUE`) to optimize  
217 computational efficiency with no appreciable losses to model performance (Appendix B;  
218 Wood *et al.*, 2015, 2017; Li & Wood, 2020). Together, the binomial HGAM and the gamma  
219 HGAM inform us on an animal's long-term average speed, since it is the product of the  
220 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)))

```

### 2.3.3 Effects of temperature on habitat selection

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

```

233 Smooth effects of percent forest cover, elevation, and distance to water accounted for  
 234 the species-level average selection strength for each resource. A random effect for each in-  
 235 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,  
 236 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource  
 237 selection (i.e., individual-level deviations from the species-level average). Tensor interaction  
 238 product terms (`ti()`) of the three resources and temperature estimated the change in re-  
 239 source selection at different temperatures. Finally, we included marginal smooth terms of  
 240 temperature to account for species- and individual-level sampling biases over temperature  
 241 (e.g., sampling more during warm periods). Detections were weighted proportionally to their  
 242 degree of independence from other temporally proximate detections (`weights = weight` –  
 243 Appendix B; Alston *et al.*, 2022), while quadrature points had a weight of 1. Quadrature  
 244 points were obtained using all raster cells in the 99.9% AKDE percentile. The number of  
 245 quadrature locations greatly outnumbered the number of observed locations (Fig. B13),  
 246 especially after accounting for weighting based on the degree of autocorrelation and the  
 247 number of home range crossings (Fig. B14).

<sup>248</sup>

### 3 Results

<sup>249</sup> Overall, 2.6% of GPS locations had temperatures lower than  $-20^{\circ}\text{C}$ , while or above  $20^{\circ}\text{C}$   
<sup>250</sup> (Table ??, Fig. B2). Species differed in overall mean probabilities of movement (range:  
<sup>251</sup> 0.05 – 0.3), mean speed when moving (range: 0.42 – 2.7 km/day), and mean distance  
<sup>252</sup> traveled (i.e.,  $P(M)$  range: 0.04 – 0.6 km/day; Table 2). Grizzly bears tended to move least  
<sup>253</sup> often (probability of moving  $P(M) \approx 0.05$ ), while wolves and cougars moved most often  
<sup>254</sup> ( $P(M) \gtrsim 0.23$ ). When moving, mountain goats and southern mountain caribou moved the  
<sup>255</sup> slowest ( $\mathbb{E}(S|M) \approx 1.44$  km/h), while wolves had the highest mean speed when moving  
<sup>256</sup> ( $\mathbb{E}(S|M) \approx 9.7$  km/h). Consequently, wolves traveled, on average, 52 km/day – 2.5 to 16.7  
<sup>257</sup> times further than other mammals.

Table 2: Mean probability of movement ( $P(M)$ ), speed when moving ( $\mathbb{E}(S)$ , km/s), and distance travelled ( $\mathbb{E}(D)$ , km/s) as estimated by models without and with temperature ( $\mathbb{E}(\dots|T)$ ), after post-stratification 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	2.04	2.06	0.33	0.34
<i>Canis lupus</i>	0.23	0.22	9.50	9.62	2.21	2.15
<i>O. americanus</i>	0.15	0.13	1.56	1.53	0.23	0.20
<i>Puma concolor</i>	0.27	0.31	2.65	2.73	0.73	0.85
<i>R. tarandus</i> (b)	0.19	0.18	2.57	2.61	0.50	0.47
<i>R. tarandus</i> (sm)	0.11	0.11	1.53	1.53	0.17	0.16
<i>U. arctos horr.</i>	0.05	0.05	2.58	2.61	0.14	0.13

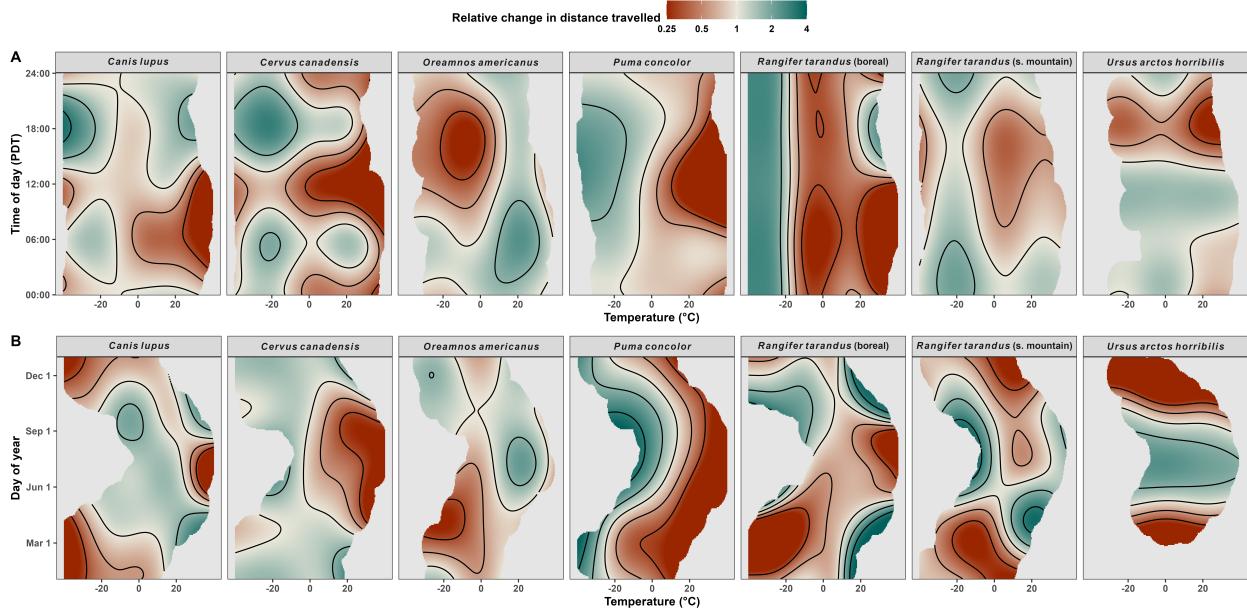
<sup>258</sup> Near  $0^{\circ}\text{C}$ , wolves preferred dense forest cover ( $\gtrsim 50\%$ ) high elevations, and distances  
<sup>259</sup> from water  $< 10$  km; elk preferred intermediate forest cover, elevations between 1 and 2 km,  
<sup>260</sup> and distances from water of 5–15 km; mountain goats preferred sparse (< 50%) forest cover,  
<sup>261</sup> elevations between 1 and 2 km; cougars preferred high forest cover, an elevation of  $\sim 1$  km,  
<sup>262</sup> and distances from water  $< 10$  km; boreal caribou selected for intermediate to high forest  
<sup>263</sup> cover, elevations near 500 m, and distances from water  $< 10$  km; southern mountain caribou  
<sup>264</sup> selected for dense forest cover, elevations near 2 km, and distances from water  $< 5$  km; and

265 grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances  
266 from water < 2 km.

267 There was relatively strong agreement between models with and without temperature  
268 (Figs. B5 and S13), but including temperature always resulted in better fits. All analyses  
269 of deviance showed that temperature significantly affected movement behavior (all p-values  
270  $< 2.2 \times 10^{-16}$ ; all  $\Delta\text{AIC} \geq 342$ ; see Table B1 and the analyses of deviance in Appendix B).  
271 The only exception to this was the mountain goat HRSF, where the addition of tempera-  
272 ture resulted in a simpler model (lower model degrees of freedom) that fit the data better  
273 (lower deviance), and hence no test was necessary to show that the inclusion of temperature  
274 produced a better fit.

### 275 3.1 Effects of temperature on movement rates

276 The effects of temperature on movement rates varied in both direction and magnitude across  
277 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
278 migration, hibernation; see Figs. B6-B8). Smooth interaction terms were well-behaved and  
279 indicated clear shifts in activity over time of day and day of year for all species. The models  
280 explained reasonably high proportions of the deviance (10.7% for the binomial model and  
281 79.3% for the Gamma model) and had good in-sample prediction (Fig. B9). All species  
282 adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 3).  
283 For example, wolves, elk, cougars, and boreal caribou reduced their mid-day and summer  
284 movement rates when temperatures were above 20°C. However, uncertainties around the  
285 estimated effects were often higher at extreme temperatures due to data scarcity. All species'  
286 estimated probability of moving decreased with sampling intervals approximately above 1  
287 hour, and most species' estimated speed when moving decreased monotonically with sampling  
288 interval, although the estimated trends were highly uncertain for some species (Fig. B10).



**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<sup>±2</sup> for ease of readability.

### 289 3.2 Effects of temperature on habitat selection

290 Species' relative selection strength (RSS) was generally strongest for elevation and weakest  
291 for forest cover, but species' RSS for resources depended on temperature. Changes in  
292 RSS with temperature were also strongest for elevation and generally weakest distance from  
293 water, but there were no common trends across all species for any of the three resources.  
294 All species, with the exception of cougars, exhibited a clear temperature-dependent shift  
295 in their preference for forest cover. At higher temperatures, wolves, mountain goats, and  
296 grizzly bears became less selective for forest cover, while elk and caribou shifted towards  
297 more intermediate forest cover without much of a change in preference width. All species  
298 shifted elevationally with temperature, although boreal caribou did not exhibit as strong of  
299 a change. As temperatures rose, elk, mountain goats, and cougars increased in elevation,  
300 while boreal wolves, southern mountain caribou, and grizzly bears decreased in elevation.  
301 Most species generally remained within 5 km of water, and temperature did not affect their  
302 selection strength as much as for the other two resources. Again, estimated RSS values were

303 generally most uncertain at extreme temperatures (Fig. B13).

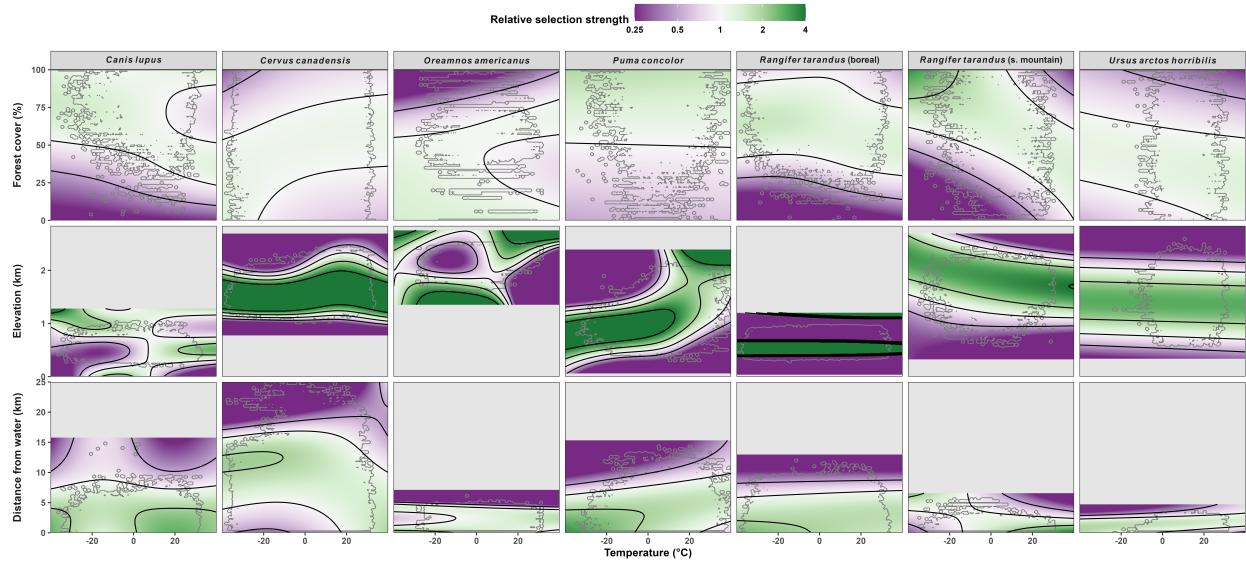
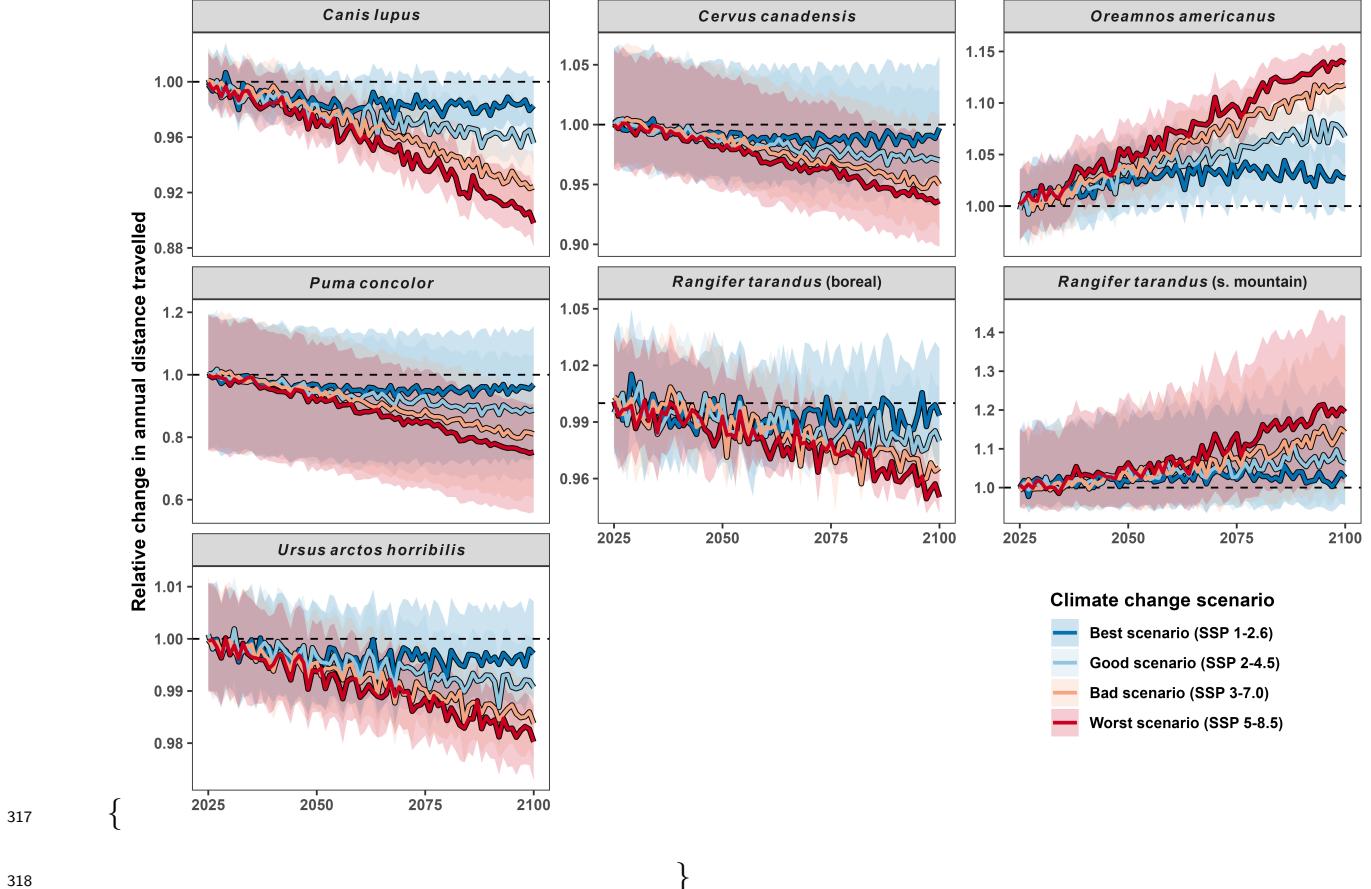


Figure 4: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were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

### 304 3.3 Predicted changes in movement during the 21<sup>st</sup> century

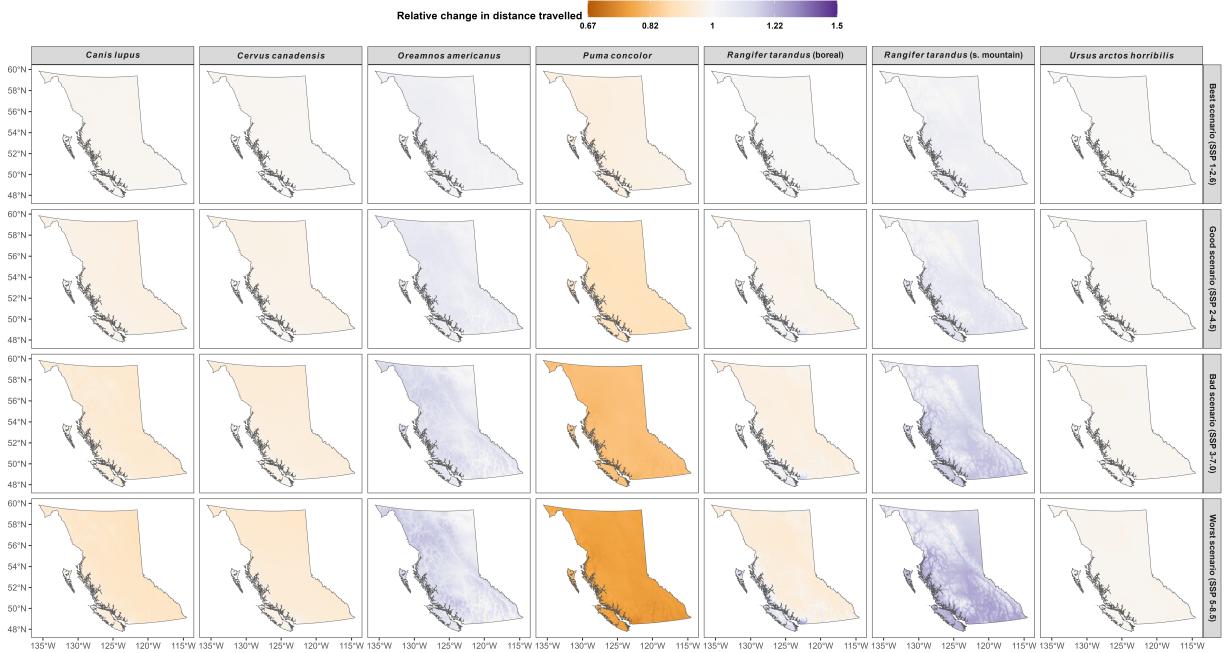
305 Species varied in both the direction and magnitude of predicted change in distance traveled,  
 306 but worse climate-change scenarios always corresponded to greater absolute changes in be-  
 307 haviour (Figs. 3.3, S11, and S12). Under the best-case scenario, absolute changes by 2100  
 308 were small (approximately 0% to 4%), while under the worst-case scenario absolute changes  
 309 ranged from ~2% (grizzly bear) to ~25% (cougars), although the models did not explicitly  
 310 account for changes in hibernation phenology. Throughout BC (Fig. 5), all species showed  
 311 little to no absolute change under the best-case scenario (approximately 0-4% relative to  
 312 2025, on average), and approximately 2-25% average absolute change under the worst-case  
 313 scenario, but the predicted changes varied spatially due to heterogeneity in climate change.  
 314 Again, absolute changes were smallest under the best-case scenario and greatest under the  
 315 worst-case scenario for all species.

316 \begin{figure}



319 \caption{The direction and magnitude of changes in movement rates due to  
 320 climate change varies among species, but worse climate-change scenarios result  
 321 in the greatest change. Lines indicate the median projected change in distance travelled  
 322 (probability of moving times speed when moving) due to changes in temperature within  
 323 the species' current extent. Shaded areas indicate the 90% prediction interval within the  
 324 range. Changes are relative to the predicted mean distances travelled in 2025 across the  
 325 four Shared Socioeconomic Pathways (SSPs). The projections only account for changes  
 326 in behaviour (i.e., movement frequency and speed) and ignore changes in  
 327 physiology or movement costs.} \end{figure}

328 We do not predict any of the species to exhibit stronger selection for their current range,  
 329 irrespective of climate change scenario. Changes in RSS by 2100 were between 0% and -3%  
 330 under the best-case scenario, but they ranged from -8% to -14% under the worst-case  
 331 scenario (Fig. 6). As with distance traveled, the change in RSS in 2100 varied throughout



**Figure 5: 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.

BC for all species (Fig. 7). All species were predicted to exhibit a decrease in RSS throughout most of BC, with the exception of boreal caribou, which had a predicted increase in approximately 67% of the province, including their current range. The increase was in great part due to the estimated increase in selection for high-elevation areas that are well outside the population's current range.

## 4 Discussion

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

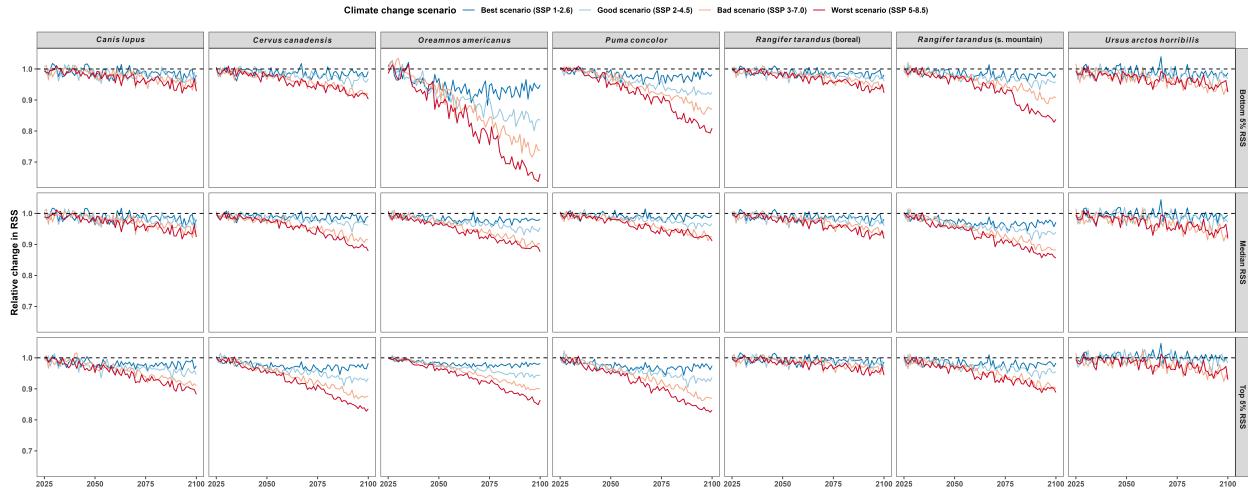


Figure 6: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in RSS for the bottom 5%, median, 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).

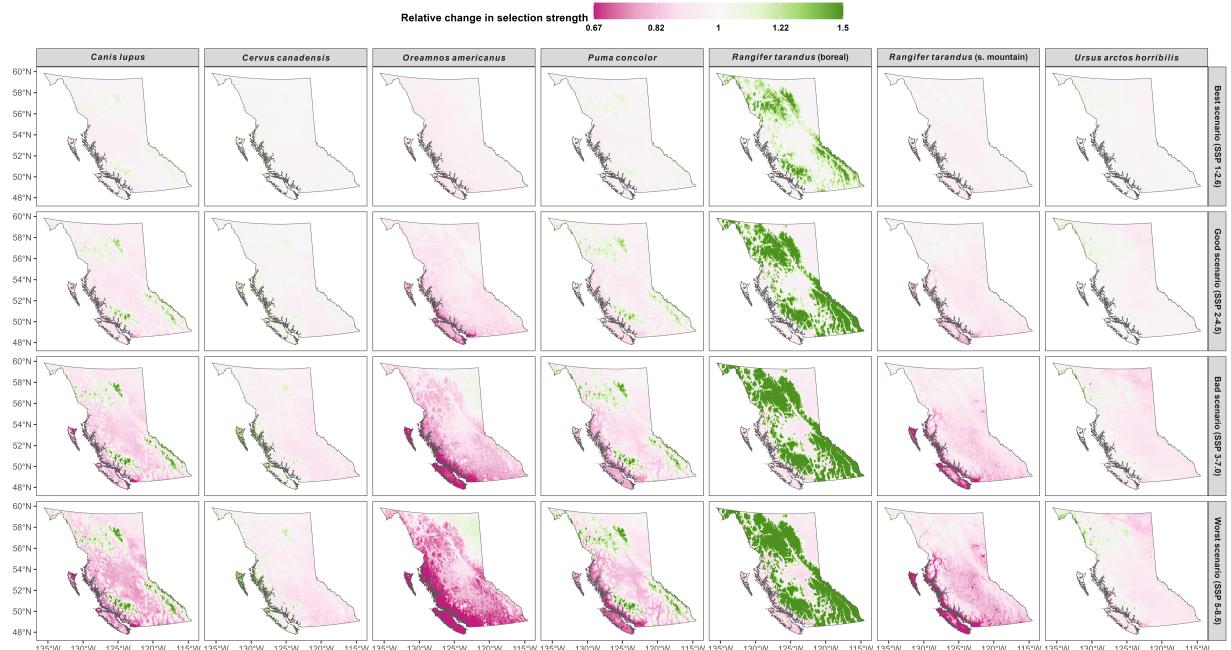


Figure 7: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios, such that 1 indicates no change, values  $< 1$  indicate 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.

increasingly frequent conditions that are both extreme and novel. Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 3 and 4 comes with substantial uncertainty, particularly given that the responses are nonlinear. At unusually warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020; Dyer *et al.*, 2023), so their movement behaviour and that of their competitors, predators, and/or prey can often be substantially different from the behaviour at typical temperatures. As extreme temperature events become more frequent and prolonged (Yao *et al.*, 2022; IPCC, 2023), mammals will be increasingly forced towards atypical behaviours that may alter community structures and behaviours, both during such events and afterwards (Logares & Nuñez, 2012; Anderson *et al.*, 2017; Zhang *et al.*, 2023). For instance, changes in climate and phenology impact the life history and behaviour of many hibernating mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality (Mortlock *et al.*, 2024) and likelihood to enter torpor (Fjelldal *et al.*, 2021). Such changes may alter the frequency and intensity of human-wildlife conflict, especially with the addition of growing pressures from human development and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et al.*, 2024). At the same time, warmer winters may reduce mammals' energetic expenditure (Berger *et al.*, 2018; Schmidt *et al.*, 2020), increase ease of movement as snow cover and depth decrease (Leclerc *et al.*, 2021; Melin *et al.*, 2023), increase their chances of finding food or being predated upon (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer *et al.*, 2022; Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*, 2009; Leclerc *et al.*, 2021; Xu *et al.*, 2021). These changes will likely have complex consequences for population and ecosystem structures and dynamics as prey, predators, and competitors experience altered seasonal cycles and increasingly common climate "weirding" (Bunnell *et al.*, 2011).

Our ability to respond to current and future changes in climate is contingent on our ability to prepare for and predict change. However, predicting animal behaviour becomes increasingly complicated as the conditions animals are exposed to deviate from current,

371 typical conditions, especially when responses are nonlinear and data are sparse.

372 Consequently, we do not present our results as a definitive guide to how mammals in BC

373 will respond to climate change. Instead, we hope they serve as a starting point to (1)

374 demonstrate that mammals' movement rates and habitat selection depend on temperature

375 and (2) how one can estimate mammals' changes in movement behaviour due to climate

376 change. Additionally, communicating uncertainty in one's estimates is crucial in assessing

377 risk probabilistically (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann,

378 2014). Recent events in global politics, including global conflicts (McNutt & Hildebrand,

379 2022; Tollefson, 2022) and the rapid rise in generative machine learning (more commonly:

380 "AI," see Roumeliotis & Tselikas, 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*,

381 2025) and its prohibitive energy and water demands (Li *et al.*, 2023) and carbon footprint

382 (Luccioni *et al.*, 2024), have placed doubt on the feasibility of reaching climate change

383 goals that seemed achievable in the past decade (United Nations Environment Programme

384 *et al.*, 2024). Mitigating climate change and its consequences will require extensive and

385 widespread collaborative effort (Huang & Zhai, 2021). Similarly, protecting a third of the

386 world's ecosystems (Section H, Targets 2 and 3 of Convention on Biological Diversity,

387 2022) appears less tangible as global political and environmental conditions change rapidly

388 and unpredictably (Sih *et al.*, 2011; Simmons *et al.*, 2021; Guenette *et al.*, 2022; Sovacool

389 *et al.*, 2023). Achieving the "30 by 30" goal will require active partnership with local

390 Peoples, especially Indigenous Peoples (Wong *et al.*, 2020; Lamb *et al.*, 2023).

391 Understanding the consequences of climate change on mammals' movement behaviour and

392 spatial distribution is a first step towards anticipating and proactively responding to future

393 changes in human-induced rapid environmental change (Sih *et al.*, 2011; Williams & Blois,

394 2018). In the following sections, we discuss the implications of our results in more detail.

395 We then expand on consequences for conservation during the 21<sup>st</sup> century and

396 considerations for future studies.

397    4.1 Effects        of            temperature        on            movement        rates

398    The lack of common effects of temperature across all species' movement rates indicates  
399    that preparing for future changes will require a variety of physiological and behavioral  
400    adaptations as ecological communities respond in complex and interconnected ways.

401    Although our models do not account for explicit physiological or phenological changes, the  
402    tensor product terms in Fig. 3 suggest that warmer temperatures cause many species to  
403    alter their daily and seasonal activity patterns (most visible in cougars and grizzly bears).  
404    For example, when temperatures were above 0°C, cougars moved most at night, but when  
405    temperatures were below 0°C they tended to move more throughout the day. Throughout  
406    the year, they adapted their tolerance to temperature and moved less when it was  
407    relatively hot (for a given time of year), especially in spring and summer. The strong  
408    reduction in the mid-day movement rates of wolves, elk, cougars, and boreal caribou when  
409    summer temperatures were above 20°C suggests that the increasingly common and intense  
410    heat waves across British Columbia will have community-wide impacts on movement rates,  
411    encounter rates, and potentially community structure (Martinez-Garcia *et al.*, 2020). More  
412    work is necessary on quantifying interspecific responses to temperature, including the  
413    effects of temperature on predation rates (but see: Cunningham *et al.*, 2021; Glass *et al.*,  
414    2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events  
415    (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of  
416    hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Morley, 2021;  
417    Carbeck *et al.*, 2022; Malpeli, 2022). However, not all species may be able to adapt at the  
418    current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018), especially since  
419    landscape changes will likely depend not only on the direct effect of temperature but also  
420    on cascading changes in the availability and unpredictability of resources (McLellan &  
421    McLellan, 2015; Pigeon *et al.*, 2016; Mezzini *et al.*, 2025).

422 **4.2 Effects of temperature on habitat selection**

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

438 **4.3 Predicted changes in movement during the 21<sup>st</sup> century**

439 Achieving the goals laid out by the “30 by 30” conservation initiative (Section H, Targets 2  
440 and 3 of Convention on Biological Diversity, 2022) will require careful planning but often  
441 also rapid action. In the case of Canada, only 13.7% of its terrestrial areas and inland  
442 waters were protected at the end of 2023 (Environment and Climate Change Canada, 2024;  
443 Minister of Environment and Climate Change, 2024). Additionally, efficient and effective  
444 conservation will require collaboration with Indigenous and local communities to ensure  
445 Treaties are respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020; e.g.,  
446 Falardeau *et al.*, 2022; Lamb *et al.*, 2023) while also actively preparing for future change  
447 (Desjardins *et al.*, 2020; Hessami *et al.*, 2021). The large range in predicted changes by

2100 (both across species and within species' current ranges) and high spatial heterogeneity in Fig. 7 highlight the need for careful planning that incorporates not only reliable estimates of change but also pragmatic and communicable measures of uncertainty and variability around such estimates. The width of the prediction intervals in Fig. 3.3 suggest that spatial and intra-individual variation should be accounted for when deciding the location and size of protected areas. Accurate estimates of the effects of changes in temperature on mammals' movement require a holistic view of the direct effects of temperature on mammals' movement directly as well as its effects on other drivers of movement, such as forage and prey availability (Mezzini *et al.*, 2025), encounter rates (Hou *et al.*, 2020; Martinez-Garcia *et al.*, 2020), population dynamics (Smith *et al.*, 2023), competitive pressure (Tórrez-Herrera *et al.*, 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation among the responses of different species (and individuals), especially as populations a rapid cascade of change (Botero *et al.*, 2015) and animals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces (Sawyer *et al.*, 2009; Sih *et al.*, 2011; Tucker *et al.*, 2018; Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*, 2024). As selection strength for current ranges changes (and likely decreases), some animals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased extinction risk (Duncan *et al.*, 2012; Logares & Nuñez, 2012; Anderson *et al.*, 2017).

468	<b>4.4 Species-specific</b>	considerations
469	<b>4.4.1 <i>Canis</i></b>	<i>lupus</i>
470	<b>4.4.2 <i>Cervus</i></b>	<i>canadensis</i>
471	<b>4.4.3 <i>Oreamnos</i></b>	<i>americanus</i>
472	<b>4.4.4 <i>Puma</i></b>	<i>concolor</i>
473	<b>4.4.5 <i>Rangifer</i></b>	<i>tarandus</i> (boreal)
474	<b>4.4.6 <i>Rangifer</i></b>	<i>tarandus</i> (s. mountain)
475	<b>4.4.7 <i>Ursus</i></b>	<i>arctos</i> <i>horribilis</i>

476 **4.5 Considerations for future studies**

477 add a section about the importance of studying smaller mammals, too

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

487 While the **ctmm** models produced scale-independent estimates of speed (i.e., model  
 488 interpretation is independent of sampling interval: Noonan *et al.*, 2019a), the accuracy,  
 489 size, and stability of speed estimates still depended on the GPS sampling frequency. This is  
 490 because coarsely-sampled movement data contains information on large-scale movements  
 491 (e.g., range crossings, migrations) but not fine-scale movements (e.g., first-order habitat

492 selection *sensu* Johnson, 1980; also see Nathan *et al.*, 2022). Using the boreal caribou as an  
493 example, the 13-hour sampling interval allows us to reasonably estimate the caribou's  
494 movement path at a temporal scale of approximately 13 hours (or greater), but we cannot  
495 produce reasonable movement trajectories at a much finer (e.g., hourly) scale.

496 Consequently, we suggest being cautious when comparing estimated movement behaviours  
497 across species, even though all predictions have been corrected to the hourly timescale by  
498 predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Thus, sampling schedules should  
499 be fine enough to reconstruct animals' movement at a sufficiently fine scale. Good estimates  
500 of an animal's speed and its movement path require telemetry locations to be taken more  
501 often than the animal's directional persistence (Noonan *et al.*, 2019a), so that, on average,  
502 the dataset contains multiple locations in between changes in direction. What constitutes a  
503 change in direction depends on what movement scale one is investigating. Small-scale  
504 movements and first-order spatial selection will require more frequent sampling than  
505 migratory movement or second- and third-order spatial selection. While `ctmm` movement  
506 models are scale-invariant in that any model can be scaled to larger or smaller areas and  
507 timescales, the model estimates are not independent of the scale of the sampling frequency.

508 When landscapes are relatively predictable across years, a larger number of sampled  
509 individuals is likely preferable over longer, multi-year telemtries. This allows one to  
510 quantify the variance across individuals, including the range of conditions and  
511 environments that individual animals are in. A good estimate of inter-individual variance  
512 provides better coefficient estimates along with more appropriate measures of uncertainty.

513 However, when conditions across years are relatively stochastic, multi-year telemtries  
514 allow one to better estimate inter-annual variation without conflating it with  
515 inter-individual differences. In either case, carefully-designed sampling schedules and  
516 (Bayesian) hierarchical models can provide good estimates of the effects of interested along  
517 with appropriate measures of uncertainty (Czado & Brechmann, 2014; McElreath, 2020).  
518 Quantifying and communicating uncertainty become particularly important as we predict

519 for conditions for which we have little to no data, such as during extreme events.

520 Additionally, estimating nonlinear trends is particularly difficult near the edges of the data

521 (e.g., extremely high temperatures), especially when data is scarce. Consequently, the

522 estimated responses at the fringes of the surfaces in figures 3 and 4 are more likely likely to

523 be poorly estimated, particularly in the case of HRSFs, but increasing data density

524 throughout the resource-temperature surfaces can ameliorate the issue. Preparing for

525 future changes requires some degree of inevitable risk, so it is imperative that models be

526 statistically sound and interpretable, and that results are communicated transparently and

527 clearly to decision makers and the public alike.

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