

Predicting how climate change will affect how and where terrestrial mammals will move in British Columbia, Canada

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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 individuals' fitness and habitat selection at the population, community, and ecosystem levels. Previous research has quantified the effects of temperature on mammalian movement behavior, but few have quantified the effects of future climate change on fine-scale movement and habitat selection. We address this gap by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on mammals' movement rates and habitat selection. We then leverage the estimated effects to predict how and where mammals will move in British Columbia (BC), Canada, throughout the 21st century. We show that changes in temperature altered movement phenology, and that climate change will impact mammals' movement rates and habitat selection throughout the century, but that there are no common trends across all study species. Consequently, we suggest that species' responses be interpreted carefully and considered jointly when extrapolating the community-level consequences of climate change.

Contents

Abstract	3
1 Introduction	5
2 Methods	9
2.1 Datasets used	9
2.1.1 GPS telemetry data	9
2.1.2 Historical and projected temperature data	9
2.1.3 Resource rasters	11
2.2 Estimating mammals' instantaneous speeds	11
2.3 Estimating the effects of temperature on mammals' movement	12
2.3.1 Disentangling direct and indirect effects	12
2.3.2 Effects of temperature on movement rates	12
2.3.3 Effects of temperature on habitat selection	14
3 Results	15
3.1 Effects of temperature on movement rates	17
3.2 Effects of temperature on habitat selection	18
3.3 Predicted changes in movement during the 21 st century	19
4 Discussion	22
4.1 Effects of temperature on movement rates	27
4.2 Effects of temperature on habitat selection	28
4.3 Predicted changes in movement during the 21 st century	29
4.4 Considerations for future studies	30
References	33

¹ 1 Introduction

² For most animals, movement is a rapid, low-cost, and low-risk response to a variety of
³ stimuli (Nathan *et al.*, 2008). Animals move to maximize resource availability (e.g., food,
⁴ water, shelter, see: Charnov, 1976; Kacelnik, Krebs & Bernstein, 1992), optimize habitat
⁵ use (Winter *et al.*, 2024), and escape predation (Peterson, Soto & McHenry, 2021; Tan *et al.*,
⁶ 2024; Bartashevich *et al.*, 2024). However, ambient temperature affects mammals' movement
⁷ rates by altering the energetic cost of movement (Taylor, Heglund & Maloij, 1982; Brown
⁸ *et al.*, 2004; Fuller *et al.*, 2016; Jahn & Seebacher, 2022), the ease of movement (e.g., snow
⁹ depth and density, see Montgomery *et al.*, 2019; Leclerc *et al.*, 2021; Melin *et al.*, 2023), and
¹⁰ the risk of overheating (Hatem *et al.*, 2014; Dyer *et al.*, 2023). Additionally, temperature
¹¹ also affects movement indirectly by through other drivers of movement behavior, such as
¹² trophic interactions (Hegel *et al.*, 2010) and the value of resources (e.g., water, heat, shelter
¹³ – see: Elmore *et al.*, 2017; Attias *et al.*, 2018; Arechavala-Lopez *et al.*, 2019). Changes in
¹⁴ temperature thus affects how animals move (e.g., movement frequency and speed – their
¹⁵ movement behavior: Nathan *et al.*, 2008; Dyer *et al.*, 2023) and where they move to (i.e.,
¹⁶ their habitat selection: Merkle *et al.*, 2016; Alston *et al.*, 2020; Giroux *et al.*, 2023).

¹⁷ Temperature also affects the consequences of animal movement, such as encounter rates
¹⁸ with resources (Mezzini *et al.*, 2024), other animals (Martinez-Garcia *et al.*, 2020), and
¹⁹ humans (Weststrate *et al.*, 2024), and these changes are exacerbated at extreme temperatures
²⁰ (Wilson *et al.*, 2001; Berger *et al.*, 2018; Giroux *et al.*, 2023). But what counts as “extreme”
²¹ varies across species: thermal specialists are more sensitive to small changes outside their
²² typical range (e.g., Giroux *et al.*, 2023), while temperature generalists can adapt more easily
²³ to change (Dupont *et al.*, 2024). However, generalists’ grater adaptability is tested when
²⁴ they are subject to changes that are more severe (McCain, 2019), affect many factors (e.g.,
²⁵ temperature, phenology, and resource availability: Polazzo *et al.*, 2024), or are too rapid to
²⁶ adapt within the span of a lifetime or a few generations (Levins, 1974; Fuller *et al.*, 2016;

Xu et al., 2021). Thus, it remains unclear how or whether species will be able to respond to climate change in the current century (Deb, Forbes & MacLean, 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 presents a need for a comprehensive understanding of (1) the direct effects of temperature on animal movement behavior and (2) the implications this will have on populations and species' adaptability and resiliency, community structure, and biodiversity at large. Recent work has documented the effects of climate change on mammals' ranges (Leclerc *et al.*, 2021), movement behavior (Melin *et al.*, 2023), thermoregulation (Mota-Rojas *et al.*, 2021), and trait-based responses (McCain, 2019), but it is still unclear how mammals will adapt their small-scale movement and habitat selection to changes in temperature during the 21st century (Intergovernmental Panel On Climate Change, 2023; but see Hetem *et al.*, 2014; Winter *et al.*, 2024). 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 and severe forest fires (Zurowski, 2023; Intergovernmental Panel On Climate Change, 2023). Over the next 100 years, these changes are expected to worsen and continue to impact mammals' fitness, movement behavior, 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, Kremsater & Wells, 2011), along with increasing anthropogenic pressure (Sawyer *et al.*, 2009; Sih, Ferrari & Harris, 2011; Weststrate *et al.*, 2024).

Understanding the direct and indirect impacts of temperature on mammalian movement is essential for decision makers to be able to prepare for and respond to change in a proactive manner (e.g., Sawyer *et al.*, 2009; McCain, 2019). The Canadian province of British Columbia is currently experiencing rapid widespread warming (Turner & Clifton, 2009; Dierauer, Allen & Whitfield, 2021), phenological shifts (Basu *et al.*, 2024; e.g., Tysor, 2025), and

54 more frequent and intense extreme events (e.g., Zhang *et al.*, 2023), including forest fires
55 (Zurowski, 2023). As we approach the deadline for the “30 by 30” conservation initiative, a
56 global effort to conserve 30% of the world’s lands and oceans by 2030 (Section H, Targets 2
57 and 3 of Convention on Biological Diversity, 2022), decision makers must understand which
58 areas will be of greatest value for maximizing the project’s effectiveness. Predicting how cli-
59 mate change will affect how, when, and where animals will move is necessary for identifying
60 which landscapes are most valuable now as well as in the future. Failing to understand how
61 changes in temperature will affect mammalian movement behavior and habitat selection will
62 hinder our ability to respond to the current climate crisis and make decisions that are viable
63 in the long term.

64 This paper provides an analysis of the effects of air temperature on the movement of
65 six terrestrial mammal species in British Columbia (BC), Canada (*Canis lupus*, *Cervus*
66 *canadensis*, *Oreamnos americanus*, *Puma concolor*, boreal and southern mountain *Rangifer*
67 *tarandus*, and *Ursus arctos horribilis*; Table 1). Using over 25 years of telemetry data
68 throughout a large spatial range of British Columbia (Fig. 1) and hourly air temperature
69 data, we estimate how mammals altered their probability of movement, speed when moving,
70 and habitat selection in response to temperature. We then pair the estimated responses with
71 climate change projections to forecast the species’ movement during the 21st century under
72 different climate-change scenarios (referred to as Shared Socioeconomic Pathways, SSPs –
73 see Riahi *et al.*, 2017). We disentangle the direct and indirect effects of temperature on the
74 movement behavior of terrestrial mammals and discuss the consequences of these changes at
75 the individual, population, and landscape levels.

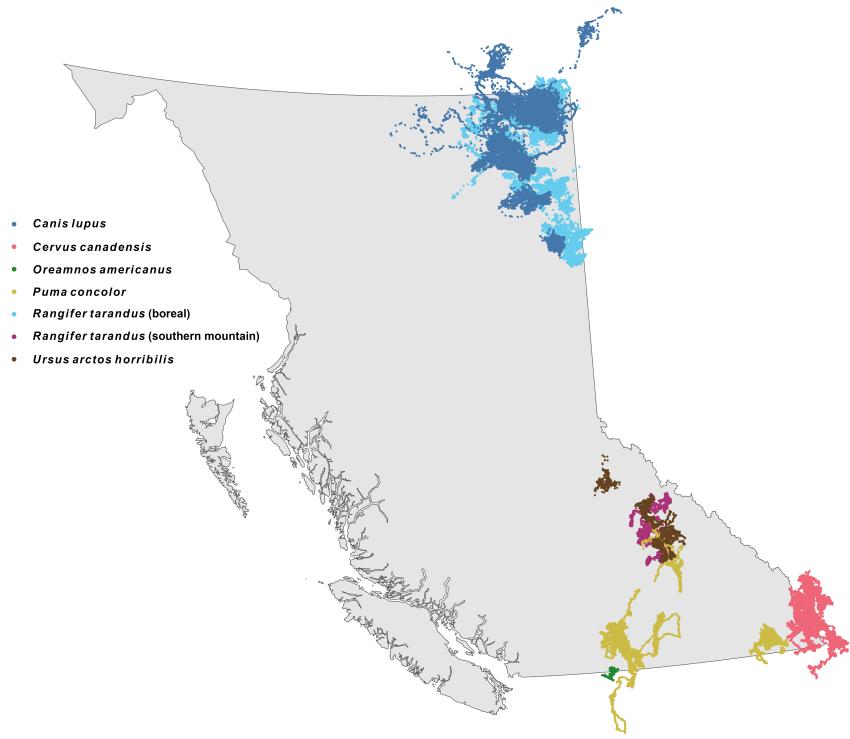


Figure 1: GPS telemetry data for the six species in this study.

Table 1: Start and end of the GPS telemetries along with the median sampling interval (Δt ; stratified by individual), number of animals (Animals), and number of animals with unresolved speed (NA speed) for each of the species in this study.

Species	Start	End	Δt (hours)	Animals	speed	NA
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25	39	0	
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00	169	0	
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.25	11	1	
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	29	0	
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	13.00	146	15	
<i>Rangifer tarandus</i> (s. mountain)	1998-03-21	2009-06-07	6.00	22	2	
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	0	

76 **2 Methods**

77 **2.1 Datasets used**

78 This manuscript leverages four main datasets: (1) a collection of GPS telemetry data;
79 (2) historical hourly reanalyzed air temperature from the ERA5 dataset from the European
80 Center for Medium-range Weather Forecasting; (3) resource rasters of percent forest cover,
81 elevation, and distance from water; and (4) climate change projections under four Shared
82 Socioeconomic Pathways (SSPs, see Riahi *et al.*, 2017). We detail the data sources and
83 analyses in the sections below.

84 **2.1.1 GPS telemetry data**

85 Elk (*Cervus canadensis*) data from Ciuti *et al.* (2012) were downloaded from Movebank
86 (study name: Elk in southwestern Alberta, see Kays *et al.*, 2022), while boreal caribou
87 (*Rangifer tarandus*) and wolf (*Canis lupus*) telemtries were acquired via a public BC Oil and
88 Gas Research and Innovation Society repository (<https://www.bcgoris.ca/projects/boreal->
89 caribou-telemetry-data). Clearly erroneous GPS locations were removed using diagnostic
90 plots of (1) distance from the median location, (2) straight-line displacement between loca-
91 tions, (3) turning angle, and (4) time interval between consecutive points. Particular atten-
92 tion was paid to points with large turning angles ($\gtrsim 170^\circ$) and excessively high straight-line
93 displacement, especially if antecedent and subsequent points indicated stationary behavior.
94 The script used to clean the data and all associated custom functions are available on GitHub
95 at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

96 **2.1.2 Historical and projected temperature data**

97 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset
98 (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting
99 server (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal tempera-

ture was estimated for each location by extracting the value from the corresponding raster cell from the temporally nearest raster using the `extract()` function from the `terra` package (version 1.7-46, Hijmans, 2023) for R (R Core Team, 2024).

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

We simulated hourly variation in weather by assuming temperature followed a normal distribution with mean specified by the monthly `climatenetR` climate projections and variance as specified by the Gamma GAMLS. We then predicted changes in movement behavior and habitat selection as a function of the simulated temperature using the HGAMs and HRSFs. For each month within each year from 2020 to 2100, we simulated hourly weather by including temperatures from the 0.1 to the 0.9 quantile by increments of 0.1, and we weighted each quantile proportionally to the (normalized) Gaussian probability density for each quantile.

125 **2.1.3 Resource rasters**

126 We estimated percent forest cover and distance from water using the rasters created by
127 Tuanmu & Jetz (2014). We calculated total forest cover by summing the temporally
128 static rasters of evergreen/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous
129 broadleaf trees, and mixed/other trees (raster classes 1-4, respectively). We converted the
130 raster of percent cover of open water (class 12) to a binary raster of pixels with water (cover
131 > 0%) or without water (cover = 0%) and then calculated each pixel's distance from the
132 nearest pixel with water using the `distance()` function from the `terra` package. Finally,
133 we obtained two digital elevation models using the `get_elev_raster()` function from the
134 `elevatr` package (version 0.99.0, Hollister *et al.*, 2023): We used a raster with a zoom
135 of 6 (0.009°) for model fitting and one with a zoom of 3 (0.08°) for downloading climate
136 change projections via `climatenar`. All final rasters and code are available on GitHub at
137 <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

138 **2.2 Estimating mammals' instantaneous speeds**

139 We modeled each animal's movement using continuous-time movement models (Fleming *et*
140 *al.*, 2014) via the `ctmm` package (version 1.2.0, Fleming & Calabrese, 2023) for `R`. We then
141 estimated mammals' instantaneous speeds by applying the `ctmm::speeds()` function on all
142 models with finite speed estimates (415 of 433, see Fleming *et al.*, 2014; Noonan *et al.*,
143 2019a). The 18 telemtries with insufficiently fine sampling were for one mountain goat, 15
144 boreal caribou, and 2 southern mountain caribou (Table 1).

145 Since `ctmm`'s movement models assume stochastic but non-zero speeds (i.e., a single,
146 stochastic moving state), data-informed speeds needed to be corrected so that the minimum
147 instantaneous speed could be 0. We performed this correction by subtracting each model's
148 mean speed while assuming speeds were χ^2 -distributed. The function we used is avail-
149 able on GitHub at [https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R)
150 `blob/main/functions/detrend_speeds.R`. To avoid artifacts due to excessively small, non-

151 zero speeds, we determined whether an animal was moving or not using the inflection point
152 of each species' histogram of detrended speed estimates, as k -nearest neighbors did not
153 discriminate between states well (Fig. S3).

154 2.3 Estimating the effects of temperature on mammals' movement

155 The following sections detail the statistical framework and modelling we used to estimate
156 the effect on temperature on mammals' movement. To assess the importance of including
157 temperature as an explicit covariate (rather than including its effects with time of day and
158 day of year), we fit models with and without smooth effects of temperature and compared
159 the deviance explained, model predictions, and AIC values of the two sets of models.

160 2.3.1 Disentangling direct and indirect effects

161 In this manuscript, we separate the effects of temperature on mammalian movement into
162 indirect and direct effects. We call "indirect" all effects that can be intervened on by altering
163 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022), and we refer to all
164 other effects as "direct". For example, an increase in temperature may push an animal to
165 prefer higher forest cover in search of shade, and conservationists can thus mitigate these
166 indirect effects of temperature on movement behavior by increasing the availability of forested
167 areas, since the effect of temperature on movement is conditional on forest cover availability.
168 In contrast, the animal may avoid moving if temperatures are above 35°C, irrespective of
169 its geographic and environmental space (*sensu* Matthiopoulos, 2022), so it is not possible to
170 mitigate the effects of temperature on movement behavior (other than changing temperature
171 directly). We provide the relevant Directed Acyclical Graphs in the Appendix (Figs. S1-S2).

172 2.3.2 Effects of temperature on movement rates

173 We estimated the effects of temperature on mammals' movement state (moving or not) and
174 speed (when moving) using two Hierarchical Generalized Additive Models (HGAMs, see

¹⁷⁵ Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version 1.9-1,
¹⁷⁶ Wood, 2017). The first HGAM estimated the probability that an animal was moving with
¹⁷⁷ a binomial family of distributions and logit link function. The second HGAM estimated an
¹⁷⁸ animal's speed (when moving) with a gamma family of distributions and log link function.
¹⁷⁹ The HGAMs included random intercepts for each animal (`s(..., bs = 're')`), fixed-effect
¹⁸⁰ intercepts for each species, and species-level `by` smooths for time of day, day of year, and
¹⁸¹ temperature (`s(..., by = species)`), see model I in Figure 4 of Pedersen *et al.*, 2019).
¹⁸² Additionally, the models had three tensor product interaction terms (`ti()`) for each species:
¹⁸³ (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and
¹⁸⁴ day of year. These three terms accounted for: (1) seasonal changes in day length, (2) hourly
¹⁸⁵ changes in the response to temperature (e.g., changes in nocturnality), and (3) seasonal
¹⁸⁶ changes in the response to temperature (e.g., changes in coats and migration timing). The
¹⁸⁷ HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines
¹⁸⁸ (`bs = 'cc'`, Wood, 2017). Together, the binomial HGAM and the gamma HGAM inform
¹⁸⁹ us on an animal's long-term average speed, since it is the product of the probability of
¹⁹⁰ moving and its average speed when moving. We fit the models with fast REML ('fREML')
¹⁹¹ and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no
¹⁹² appreciable losses to model performance (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017;
¹⁹³ Li & Wood, 2020). Additional details are provided in Appendix A.

```

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)))

```

194 2.3.3 Effects of temperature on habitat selection

195 We estimated the effects of temperature on each species' selection for percent forest cover,
 196 elevation, and distance from water by fitting a Hierarchical Resource Selection Function for
 197 each species using an HGAM with a Poisson family of distributions and log link function (Ap-
 198 pendix B, also see Aarts *et al.*, 2008). We accounted for the spatiotemporal autocorrelation
 199 in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
 200 Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b) to produce
 201 estimates of second- and third-order habitat selection (*sensu* Johnson, 1980). While we rec-
 202 ognize there are other important drivers of habitat selection (e.g., forest age, forest type,
 203 prey availability), we decided to only use these three proxies to produce results that are
 204 comparable between species and to make province-wide predictions simpler. Each species'
 205 model had the same structure:

```

rsf <- bam(
  detected ~ # 1 for telemetry locations, 0 for quadrature data
  # 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, temperature_C, k = 6, bs = 'tp') +
  ti(elevation_m, temperature_C, k = 6, bs = 'tp') +
  ti(dist_water_m, temperature_C, k = 6, bs = 'tp') +
  # include marginals of temperature to remove sampling biases
  s(temperature_C, k = 4, bs = 'tp') +
  s(temperature_C, animal, k = 4, bs = 'fs', xt = list(bc = 'cr')),
  family = poisson(link = 'log'),
  data = d,
  weights = weight, # based on AKDE
  method = 'fREML',
  discrete = TRUE)

```

Smooth effects of percent forest cover, elevation, and distance to water accounted for the species-level average selection strength for each resource. A random effect for each individual animal corrected for uneven sampling across individuals, while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource selection (i.e., individual-level deviations from the species-level average). Tensor interaction product terms (`ti()`) of the three resources and temperature estimated the change in resource selection at different temperatures. Finally, we included marginal smooth terms of temperature to account for species- and individual-level sampling biases over temperature (e.g., sampling more during warm periods). Detections were weighted proportionally to their degree of independence from other temporally proximate detections (`weights = weight` – see Appendix B and Alston *et al.*, 2022), while quadrature points had a weight of 1.

3 Results

Data were relatively scarce for temperatures lower than -20°C or above 20°C (Fig. S4). Species differed in overall mean probabilities of movement (range: 0.05 – 0.3), mean speed when moving (range: 0.42 – 2.7 km/day), and mean distance traveled (range: 0.04 – 0.6 km/day), even after predicting for one-hour time intervals for all species (Table 2). Grizzly

222 bears tended to move least often (probability of moving $P(M) \approx 0.05$), while wolves and
223 pumas moved most often ($P(M) \gtrapprox 0.23$). When moving, mountain goats and southern
224 mountain caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.4$ m/s), while wolves had the highest
225 mean speed when moving ($\mathbb{E}(S|M) \approx 2.7$ m/s). Consequently, wolves traveled, on average,
226 50 km/day – 2.5 to 16.7 times further than other mammals.

Table 2: Mean probability of movement ($P(M)$), speed when moving ($\mathbb{E}(S)$), and distance travelled ($\mathbb{E}(D)$) as estimated by models without and with temperature ($(\dots|T)$), after post-stratifying to a 1-hour sampling rate and a temperature of $T = 0^\circ\text{C}$.

Species	$P(M)$	$P(M T)$	$\mathbb{E}(S)$	$\mathbb{E}(S T)$	$\mathbb{E}(D)$	$\mathbb{E}(D T)$
<i>Canis lupus</i>	0.23	0.22	2.64	2.67	0.61	0.60
<i>Cervus canadensis</i>	0.16	0.17	0.57	0.57	0.09	0.10
<i>Oreamnos 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> (boreal)	0.19	0.18	0.71	0.73	0.14	0.13
<i>R. tarandus</i> (s. mountain)	0.11	0.11	0.43	0.42	0.05	0.05
<i>Ursus arctos horribilis</i>	0.05	0.05	0.72	0.72	0.04	0.04

227 At average temperatures, wolves preferred dense forest cover ($\gtrapprox 50\%$) high elevations,
228 and distances from water < 10 km; elk preferred intermediate forest cover, elevations between
229 1 and 2 km, and distances from water of 5-15 km; mountain goats preferred sparse (< 50%)
230 forest cover, elevations between 1 and 2 km; pumas preferred high forest cover, an elevation
231 of ~ 1 km, and distances from water < 10 km; boreal caribou selected for intermediate to high
232 forest cover, elevations near 500 m, and distances from water < 10 km; southern mountain
233 caribou selected for dense forest cover, elevations near 2 km, and distances from water <
234 5 km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and
235 distances from water < 2 km.

236 Including temperature in the models always increased within-sample prediction, but the
237 change was not always substantial (deviance explained increased between 0.2% and 18.6%,

238 with all HRSFs having an increase ≥ 4.6), and there was relatively strong agreement between
239 models with and without temperature (Figs. S5 and S13), but including temperature resulted
240 in substantially better fits for all models, especially HRSFs (all $\Delta\text{AIC} \leq -342$; Table 3).

Table 3: Changes in deviance explained (ΔDE) and Akaike Information Criterion (ΔAIC) from including temperature in the models estimating probability of movement ($P(\text{moving})$) and speed when moving (Speed) as well as in species-level Hierarchical Resource Selection Functions (HRSF).

Model	Species	ΔDE	ΔAIC
P(moving)	All	0.5%	-5927
Speed	All	0.2%	-1682
HRSF	Canis lupus	9.2%	-6566
HRSF	Cervus canadensis	4.6%	-4448
HRSF	Oreamnos americanus	18.6%	-813
HRSF	Puma concolor	8%	-966
HRSF	Rangifer tarandus (boreal)	5.3%	-5637
HRSF	Rangifer tarandus (s. mountain)	12%	-342
HRSF	Ursus arctos horribilis	17.7%	-914

241 **3.1 Effects of temperature on movement rates**

242 The effects of temperature on movement rates varied in both direction and magnitude across
243 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,
244 migration, hibernation; see Figs. S6-S8). Smooth interaction terms were well-behaved and
245 indicated clear shifts in activity over time of day and day of year for all species. The models
246 explained reasonably high proportions of the deviance (10.7% for the binomial model and
247 79.3% for the Gamma model) and had good in-sample prediction (Fig. S9). All species
248 adapted their daily and seasonal movement behavior to changes in temperature (Fig. 2).
249 Wolves, elk, pumas, and boreal caribou reduced their mid-day and summer movement rates

250 when temperatures were above 20°C. However, uncertainties around the estimated effects
251 were often higher at extreme temperatures due to data scarcity.

252 All species' estimated probability of moving decreased with sampling intervals approx-
253 imately above 1 hour, and most species' estimated speed when moving decreased mono-
254 tonically with sampling interval, although the estimated trends were highly uncertain for
255 some species (Fig. S10). While the `ctmm` models produced scale-independent estimates of
256 speed (i.e., model interpretation is independent of sampling interval: Noonan *et al.*, 2019a),
257 the accuracy, size, and stability of speed estimates still depended on the GPS sampling fre-
258 quency. This is because coarsely-sampled movement data contains information on large-scale
259 movements (e.g., range crossings, migrations) but not fine-scale movements (e.g., first-order
260 habitat selection *sensu* Johnson, 1980; also see Nathan *et al.*, 2022). Using the boreal caribou
261 as an example, the 13-hour sampling interval allows us to reasonably estimate the caribou's
262 movement path at a temporal scale of approximately 13 hours (or greater), but we cannot
263 produce reasonable movement trajectories at a much finer (e.g., hourly) scale. Consequently,
264 we suggest being cautious when comparing estimated movement behaviors across species,
265 even though all predictions have been corrected to the hourly timescale by predicting for
266 1-hour time intervals (i.e., `dt_hours = 1`).

267 3.2 Effects of temperature on habitat selection

268 The number of available points greatly outnumbered the number of used points (Fig.
269 S14), especially after accounting for weighting based on the degree of autocorrelation and
270 the number of home range crossings (Fig. S14). Species' relative selection strength (RSS)
271 for resources depended on temperature, and RSS was generally strongest for elevation and
272 weakest for forest cover. Changes in RSS with temperature were also strongest for elevation
273 and generally weakest distance from water, but there were no common trends across all
274 species for any of the three resources. All species, with the exception of pumas, exhibited
275 a clear temperature-dependent shift in their preference for forest cover. At higher tempera-

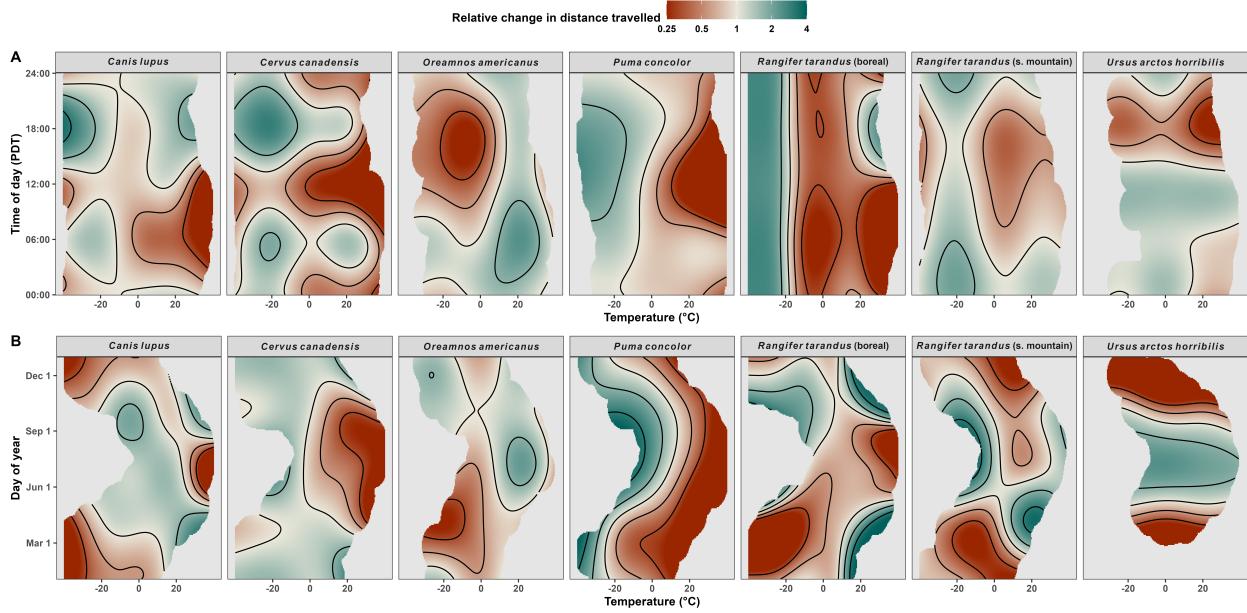


Figure 2: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**B**). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the log₂ scale to help visualize patterns in doubling, and values are capped to -75% and +300% (i.e., $2^{\pm 2}$) for ease of readability.

tures, wolves, mountain goats, and grizzly bears became less selective for forest cover, while elk and caribou shifted towards more intermediate forest cover without much of a change in preference width. All species shifted elevationally with temperature, although boreal caribou did not exhibit as strong of a change. As temperatures rose, elk, mountain goats, and pumas increased in elevation, while boreal wolves, southern mountain caribou, and grizzly bears decreased in elevation. Most species generally remained within 5 km of water, and temperature did not affect their selection strength as much as for the other two resources. Estimated RSS values were generally most uncertain at extreme temperatures (Fig. S13).

3.3 Predicted changes in movement during the 21st century

Species varied in both the direction and magnitude of predicted change in distance travelled, but worse climate-change scenarios always corresponded to greater absolute changes in behavior (Figs. 4, S11, and S12). Under the best-case scenario, absolute changes by 2100 were small (approximately 0% to 4%), while under the worst-case scenario absolute changes ranged from ~2% (grizzly bear) to ~25% (pumas), although the models did not explicitly

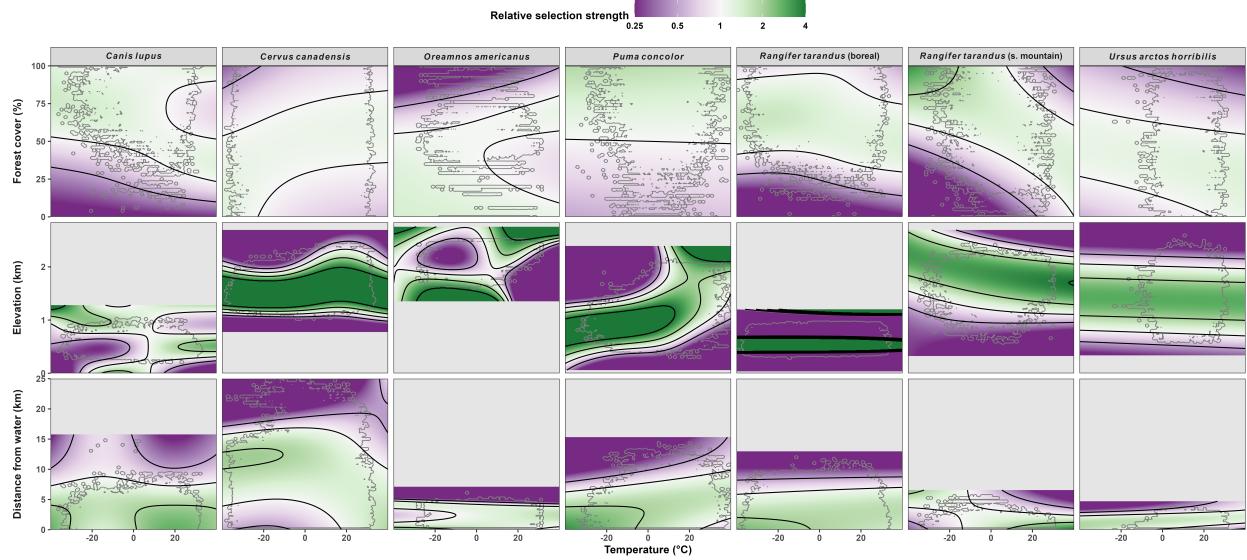


Figure 3: Temperature strongly affects mammals' habitat selection. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were re-centered and capped to $2^{\pm 2}$ to improve readability.

account for changes in hibernation phenology. Throughout BC (Fig. 5), all species showed little to no absolute change under the best-case scenario (approximately 0-4% relative to 2025, on average), and approximately 2-25% average absolute change under the worst-case scenario, but the predicted changes varied spatially due to heterogeneity in climate change. Again, absolute changes were smallest under the best-case scenario and greatest under the worst-case scenario for all species.

All species exhibited a decrease in RSS within their current range, irrespective of climate change scenario. Changes were often only between -1% and -3% under the best-case scenario but they ranged from -8% to -14% under the worst-case scenario (@ref:fig(t-hrsfs)). As with distance traveled, the change in RSS in 2100 varied throughout 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 decrease in approximately 37% 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.

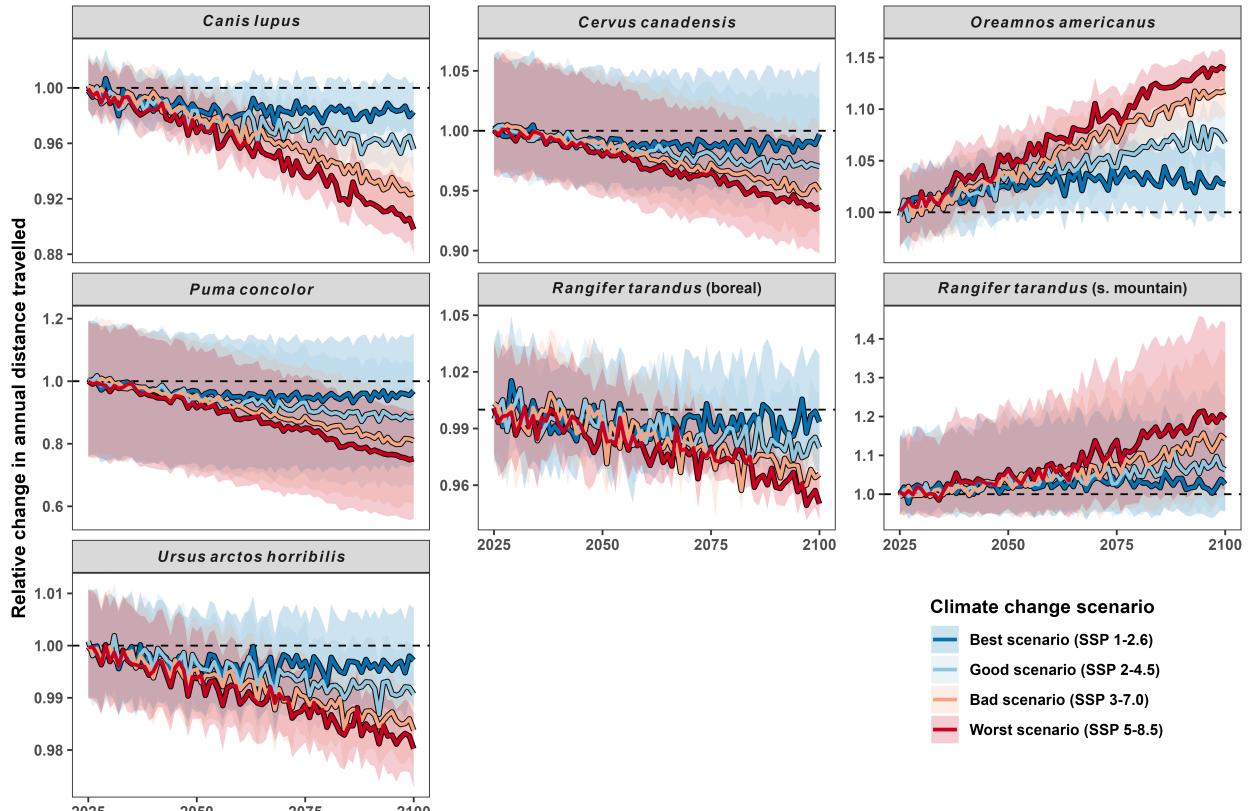


Figure 4: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change.** Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to 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 behavior (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

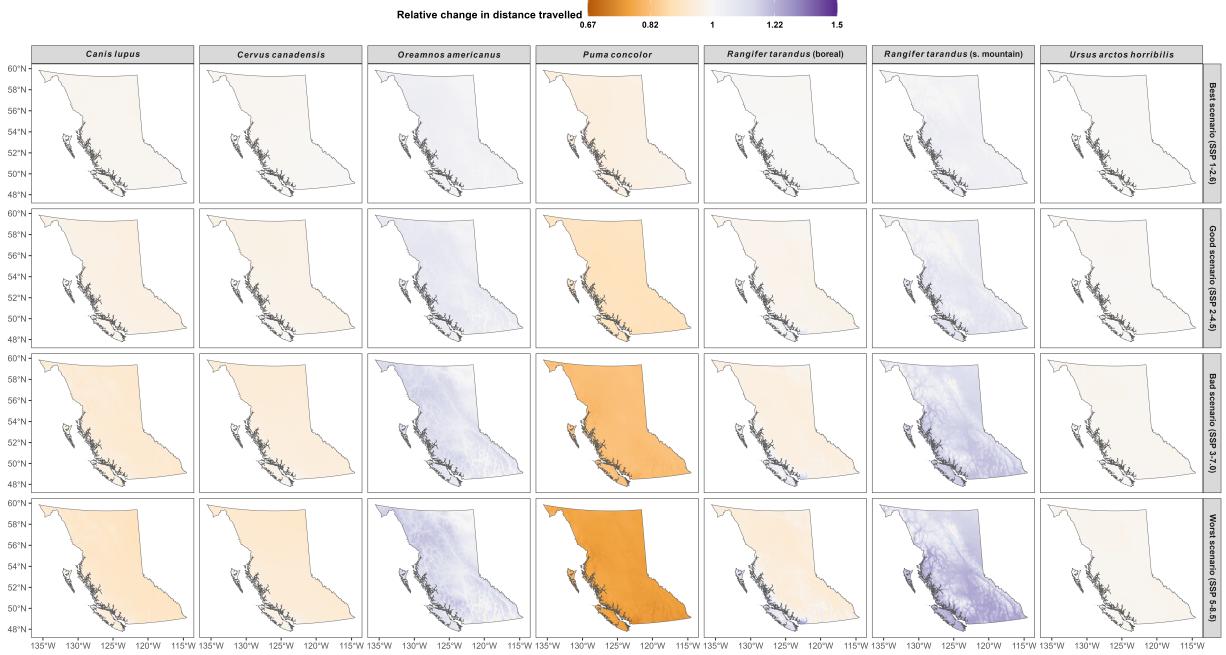


Figure 5: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, 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 0.8 and 1.25 ($\approx 2^{0.58}$; 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.

305 4 Discussion

306 We have demonstrated that temperature is an important determinant of how and where
 307 mammals move, even while accounting for seasonality (e.g., changes in photoperiod, hor-
 308 mones, and resources). Disentangling temperature from other drivers allowed us to predict
 309 how changes in climate will affect mammalian movement even if all other drivers remain
 310 approximately constant or adapt at negligible rates. However, predicting mammals' re-
 311 sponds to climate change becomes increasingly complex as habitats warm and animals are
 312 exposed to increasingly frequent conditions that are both extreme and novel. Predicting at
 313 mammals' responses at the data-scarce fringes of the surface plots in Figs. 2 and 3 comes
 314 with substantial uncertainty, particularly given that the responses are nonlinear. At unusu-
 315 ally warm temperatures, mammals (and other homeotherms) overheat (Alston *et al.*, 2020;
 316 Dyer *et al.*, 2023), so their movement behavior and that of their competitors, predators,
 317 and/or prey can often be substantially different from the behavior at typical temperatures.

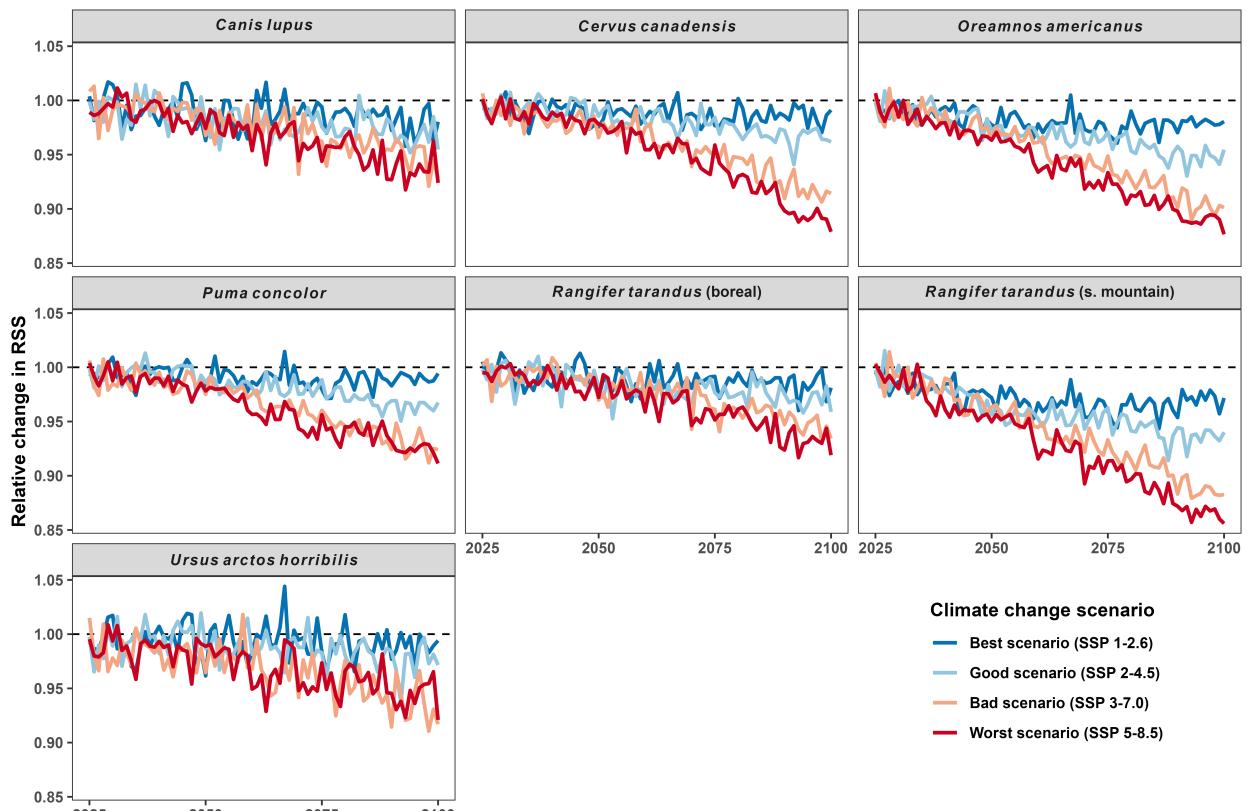


Figure 6: **All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario.** Lines indicate the projected change in RSS for the bottom 5%, median,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

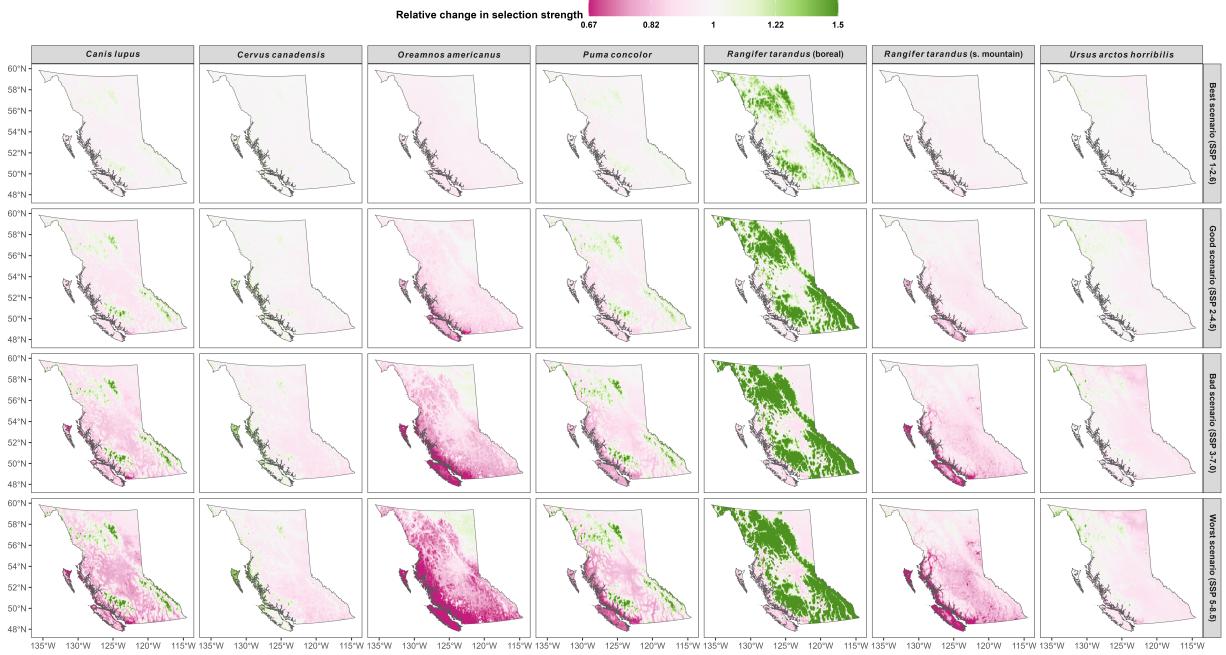


Figure 7: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, 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 ($\approx 2^{\pm 0.6}$; 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.

As extreme temperature events become more frequent and prolonged (Yao *et al.*, 2022; Intergovernmental Panel On Climate Change, 2023), mammals will be increasingly forced to atypical behaviors, which will have the potential to substantially alter community structures and behaviors, both during such events and afterwards (Zhang *et al.*, 2023). For instance, changes in climate and phenology impact the life history and behavior of many hibernating mammals (Wells *et al.*, 2022), and hot weather can also affects mammals' sleep quality (e.g., wild boars, *Sus scrofa*: Mortlock *et al.*, 2024) and likelihood to enter torpor (e.g., Australian eastern long-eared bat, *Nyctophilus bifasciatus*: Fjelldal, Wright & Stawski, 2021). Our results show that warmer temperatures cause grizzly bears to move further earlier in the year (Fig. 2), which 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 their ability to find food or be predated upon (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen

³³² *et al.*, 2021; Slatyer, Umbers & Arnold, 2022; Sullender *et al.*, 2023), and affect the timing
³³³ and duration of migrations (Sawyer *et al.*, 2009; Xu *et al.*, 2021; Leclerc *et al.*, 2021) as
³³⁴ well as the overall ease of movement as snow cover and depth decrease (Leclerc *et al.*, 2021;
³³⁵ Melin *et al.*, 2023). These changes will likely have complex consequences for population and
³³⁶ ecosystem structures and dynamics as prey, predators, and competitors experience altered
³³⁷ seasonal cycles and increasingly common climate “weirding” (Bunnell *et al.*, 2011), includ-
³³⁸ ing warmer temperatures and more frequent and intense extreme events (Yao *et al.*, 2022;
³³⁹ Intergovernmental Panel On Climate Change, 2023), such as heat waves, cold spells, floods
³⁴⁰ and droughts, plant and animal die-offs, and sudden growth surges (sometimes referred to
³⁴¹ as “black swan” events – see: Logares & Nuñez, 2012; Anderson *et al.*, 2017).

³⁴² Our success in respond to current and future changes in climate is contingent on our
³⁴³ ability to prepare for and predict change. However, predicting animal behavior becomes
³⁴⁴ increasingly complicated as the conditions animals are exposed to deviate from current, typ-
³⁴⁵ ical conditions, especially when responses are nonlinear. Consequently, we do not present
³⁴⁶ our results as a definitive guide to how mammals in BC will respond to climate change. In-
³⁴⁷ stead, we hope they serve as a starting point to (1) demonstrate that mammals’ movement
³⁴⁸ rates and habitat selection depend on temperature and (2) how one can estimate mammals’
³⁴⁹ changes in movement behavior due to climate change. An important limitation of Figs. 2
³⁵⁰ and 3 is that we do not include measures of uncertainty around the estimated responses, as
³⁵¹ they cannot be incorporated easily in surface plots, and the purpose of the figures was to
³⁵² illustrate the magnitude and direction of the responses rather than contrasting the surfaces
³⁵³ against some hypotheses. Still, we stress that uncertainty is crucial in producing transparent
³⁵⁴ and informed results, particularly when using such estimates for decision-making or predict-
³⁵⁵ ing future changes, as we do in Figs. 4 and 6. We present the spatial estimates of distance
³⁵⁶ traveled and relative habitat selection strength in 2100 without measures of uncertainty for
³⁵⁷ conciseness, but we suggest that future studies and reports include some form of compati-
³⁵⁸ bility intervals (Gelman & Greenland, 2019), whether these be Bayesian Credible intervals

359 (McElreath, 2020) or Frequentist Confidence Intervals, although the latter do not provide
360 a measure of uncertainty in the common sense of the word (Morey *et al.*, 2016; Amrhein,
361 Greenland & McShane, 2019). As alternatives to heat-map surface plots, one may include
362 compatibility intervals using faceted or perspective plots of the surfaces along with the inter-
363 vals (e.g., Fig. 5 in Akkaya Hocagil *et al.*, 2024) or overlapping contour plots on the surfaces
364 (e.g., Fig. 4.14 on page 187 of Wood, 2017). For a simpler figure, one could also include
365 lines with compatibility intervals for the responses at different temperatures.

366 How to represent uncertainty may seem trivial to some, but communicating uncertainty
367 is crucial in assessing risk probabilistically (Aven & Kvaløy, 2002; Ayre & Landis, 2012;
368 Czado & Brechmann, 2014). Recent events in global politics, including global conflicts
369 (McNutt & Hildebrand, 2022; Tollefson, 2022) and the rapid rise in generative machine
370 learning (also referred to as artificial intelligence and GenAI, see Roumeliotis & Tsilikas,
371 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*, 2025) and its prohibitive energy and
372 water demands (Li *et al.*, 2023) and carbon footprint (Luccioni, Viguier & Ligozat, 2024),
373 have placed doubt on the likelihood and feasibility of reaching climate change goals that
374 seemed achievable in the past decade (United Nations Environment Programme *et al.*, 2024).
375 Maintaining global warming below 1.5 or even 2.0°C has been questioned (United Nations
376 Environment Programme *et al.*, 2024), and mitigating climate change will require extensive
377 and widespread collaborative effort (e.g., Huang & Zhai, 2021). Similarly, protecting a third
378 of the world's terrestrial and aquatic ecosystems (Section H, Targets 2 and 3 of Convention
379 on Biological Diversity, 2022) appears less tangible as global political and environmental
380 conditions change rapidly and unpredictably (Sih *et al.*, 2011; Simmons, Nolte & McGowan,
381 2021; Guenette, Kenworthy & Wheeler, 2022; Sovacool, Baum & Low, 2023), and achieving
382 such a goal will require active collaboration with local Peoples, especially Indigenous Peoples
383 (Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences of climate change on
384 mammals' movement behavior and spatial distribution (Williams & Blois, 2018) is a first step
385 towards anticipating and proactively responding to future changes in human-induced rapid

386 environmental change (Sih *et al.*, 2011), including climate change. In the following sections,
387 we discuss the implications of our results in more detail. We then expand on consequences
388 for conservation during the 21st century and considerations for future studies.

389 **4.1 Effects of temperature on movement rates**

390 The lack of common effects of temperature across all species' movement rates indicates that
391 responding to current conditions and preparing for future changes will require a variety
392 of adaptations as communities adapt and respond in complex and interconnected ways.
393 Although our models do not account for any physiological or explicit phenological changes
394 (e.g., in the timing of sleep and hibernation), the tensor product terms in Fig. 2 suggest that
395 warmer temperatures cause many species to alter their daily and seasonal activity patterns
396 (most visible in pumas and grizzly bears). For example, when temperatures were above 0°C,
397 pumas moved most at night, but when temperatures were below 0°C they tended to move
398 more throughout the day. Throughout the year, they adapted their tolerance to temperature
399 and moved less when it was relatively hot (for a given time of year), especially in spring
400 and summer. The strong reduction in wolves', elk's, pumas', and boreal caribou's mid-day
401 movement rates when summer temperatures are above 20°C suggests that the increasingly
402 common and intense heat waves across British Columbia will have community-wide impacts
403 on movement rates, encounter rates, and potentially community structure (Martinez-Garcia
404 *et al.*, 2020). More work is necessary on interspecific responses to temperature, including the
405 effects of temperature on predation rates (Glass *et al.*, 2021; but see: Cunningham, Gardner
406 & Martin, 2021; Brivio *et al.*, 2024). As indicated by grizzly bears' tendency to travel
407 greater distances earlier in the year with increasing temperatures, the increase in intensity
408 and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely
409 also impact the occurrence and timing of hibernation (Wells *et al.*, 2022) and migration or
410 seasonal range expansions (Morley, 2021; Malpeli, 2022; Carbeck *et al.*, 2022). This change
411 will likely depend not only on the direct effect of temperature but also on cascading changes

⁴¹² in the availability and unpredictability of resources (McLellan & McLellan, 2015; Pigeon,
⁴¹³ Stenhouse & Côté, 2016; Mezzini *et al.*, 2024).

⁴¹⁴ The greater uncertainty around the estimated movement rates at temperatures outside
⁴¹⁵ the typical temperatures for a given day (Figs. S4, S6-S8) highlights the importance of
⁴¹⁶ including appropriate measures of uncertainty when evaluating the consequences of climate
⁴¹⁷ change on mammals' movement behavior. In this paper, we present our results cognizantly of
⁴¹⁸ the lack of uncertainty measures in many of our figures: We hoped to demonstrate how mam-
⁴¹⁹ malian movement behavior depends on temperature while presenting the need for additional
⁴²⁰ research. We expand on the importance of quantifying and communicating uncertainty in
⁴²¹ the last section of this discussion. Our relatively simple models indicate that changes in tem-
⁴²² perature will alter movement behavior even without accounting for large-scale physiological
⁴²³ and behavioral adaptations, which may not be possible at the current rate of climate change
⁴²⁴ (Heten *et al.*, 2014; Williams & Blois, 2018). Still, our models to indicate that some animals
⁴²⁵ adapt their behavior phenology in response to temperature, as indicated by wolves', elk's,
⁴²⁶ caribou's, and grizzly bears' increased movement rates during warmer winters and spring
⁴²⁷ days.

⁴²⁸ 4.2 Effects of temperature on habitat selection

⁴²⁹ As with the effects of temperature on movement rates, the lack of common effects of
⁴³⁰ temperature across all species indicates that efficient and proactive habitat conservation
⁴³¹ will require taxonomic nuance. In particular, our HRSFs do not account for any explicit
⁴³² physiological responses to temperature that may impact movement such as changes in the
⁴³³ phenology of plants, ice, or mammalian physiology or behavior (e.g., seasonal coats, seasonal
⁴³⁴ migration) other than as direct responses to temperature. Consequently, the behavioral
⁴³⁵ changes we present should be interpreted carefully. While some seasonal cycles do not depend
⁴³⁶ directly on temperature and may thus not be impacted directly by climate change (such as
⁴³⁷ those driven by photoperiod, see Liu *et al.*, 2022), the predictions we present also rely on

the assumption that mammals will not adapt these seasonal cycles based on temperature-dependent cues, such as weather (Xu & Si, 2019) or forage availability (Middleton *et al.*, 2018). Additionally, it is important to stress the distinction between habitat selection and quality. While animals tend to select for high-quality habitats (e.g., Wright, 2024), high selection strength can also be a consequence of an ecological trap, an area animals are attracted to that provides a net loss of fitness rather than a gain (Swearer *et al.*, 2021; Zuñiga-Palacios *et al.*, 2021).

4.3 Predicted changes in movement during the 21st century

Achieving the goals laid out by the “30 by 30” conservation initiative (Section H, Targets 2 and 3 of Convention on Biological Diversity, 2022) will require careful planning but often also rapid action. In the case of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the end of 2023 (An act respecting transparency and accountability in relation to certain commitments canada has made under the convention on biological diversity, 2024; Environment and Climate Change Canada, 2024). Additionally, efficient and effective conservation will require collaboration with Indigenous and local communities to ensure Treaties are respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020; e.g., Falardeau *et al.*, 2022; Lamb *et al.*, 2023) while also actively preparing for future change (Desjardins, Friesen & Jordan, 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 figure 7 highlight the need for careful planning that incorporates not only accurate estimates of change but also pragmatic and communicable measures of uncertainty and variability around such estimates. The width of the prediction intervals in Figure 4 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 availability (Mezzini *et al.*, 2024), population dynamics (**needs_ref?**), competitive pressure (e.g., Tórrez-Herrera, Davis & Crofoot, 2020), and predation risk (Kohl *et al.*, 2019). This complexity results in the great variation among the responses of different species (and individuals). 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 suffer a decrease in fitness and an increase in extinction risk (Duncan *et al.*, 2012).

Together, the predicted changes in distance traveled and habitat selection indicate that climate change will have complex consequences for populations as well as cascade effects within ecosystems as species adapt to the changing environments (or fail to do so: Botero *et al.*, 2015; Polazzo *et al.*, 2024). The resulting changes in mammalian movement behavior will have ramifications in individuals' encounter rates (Martinez-Garcia *et al.*, 2020; Hou *et al.*, 2020), population dynamics (**needs_ref?**), and food webs (**needs_ref?**) as landscapes change and animals face increasing pressures from human activity (Sih *et al.*, 2011), including habitat fragmentation (**needs_ref?**), habitat loss (**needs_ref?**), and greater human presence in wild spaces (Rice, 2022; Rosenthal *et al.*, 2022; Weststrate *et al.*, 2024).

480 **Cite Tucker et al. (2018)**

481 **4.4 Considerations for future studies**

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

490 address each consideration in the following three paragraphs.

491 Sampling schedules should be fine enough to reconstruct animals' movement at a suf-
492 ficiently fine scale. Good estimates of an animal's speed and its movement path require
493 telemetry locations to be taken more often than the animal's directional persistence (Noo-
494 nan *et al.*, 2019a), so that, on average, the dataset contains multiple locations in between
495 changes in direction. What constitutes a change in direction depends on what movement
496 scale one is investigating. Small-scale movements and first-order spatial selection will re-
497 quire more frequent sampling than migratory movement or second- and third-order spatial
498 selection. While `ctmm` movement models are scale-invariant in that any model can be scaled
499 to larger or smaller areas and timescales, the model estimates are not independent of the
500 scale of the sampling frequency.

501 When landscapes are relatively predictable across years, a larger number of sampled in-
502 dividuals is likely preferable over longer, multi-year telemtries. This allows one to quantify
503 the variance across individuals, including the range of conditions and environments that
504 individual animals are in. A good estimate of inter-individual variance provides better co-
505 efficient estimates along with more appropriate measures of uncertainty. However, when
506 conditions across years are relatively stochastic, multi-year telemtries allow one to better
507 estimate inter-annual variation without conflating it with inter-individual differences. In
508 either case, carefully-designed sampling schedules and (Bayesian) hierarchical models can
509 provide good estimates of the effects of interested along with appropriate measures of un-
510 certainty (McElreath, 2020).

511 Quantifying and communicating uncertainty become particularly important as we predict
512 for conditions for which we have little to no data, such as during extreme events. Addition-
513 ally, estimating nonlinear trends is particularly difficult near the edges of the data (e.g.,
514 extremely high temperatures), especially when data is scarce. Consequently, the estimated
515 responses at the fringes of the surfaces in figures 2 and 3 are more likely likely to be poorly
516 estimated, particularly in the case of HRSFs, but increasing data density throughout the

517 resource-temperature surfaces can ameliorate the issue. Preparing for future changes re-
518 quires some degree of inevitable risk, so it is imperative that models be statistically sound
519 and interpretable, and that results are communicated transparently and clearly to decision
520 makers and the public alike.

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