

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

Stefano Mezzini^{1,2} Chris H. Fleming^{3,4} Siobhan Darlington^{1,2}

Adam T. Ford^{1,2} Karen E. Hodges^{1,2} Kirk Safford⁵

Robert Serrouya^{1,2,6} Michael J. Noonan^{1,2,7}

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

² Department of Biology, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

³ Department of Biology, University of Central Florida, Orlando, Florida 32816, United States.

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

⁵ BC Parks

⁶ Wildlife Science Centre, Biodiversity Pathways, University of British Columbia Okanagan, Revelstoke, British Columbia, Canada.

⁷ Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, 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.

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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 (Heten *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.

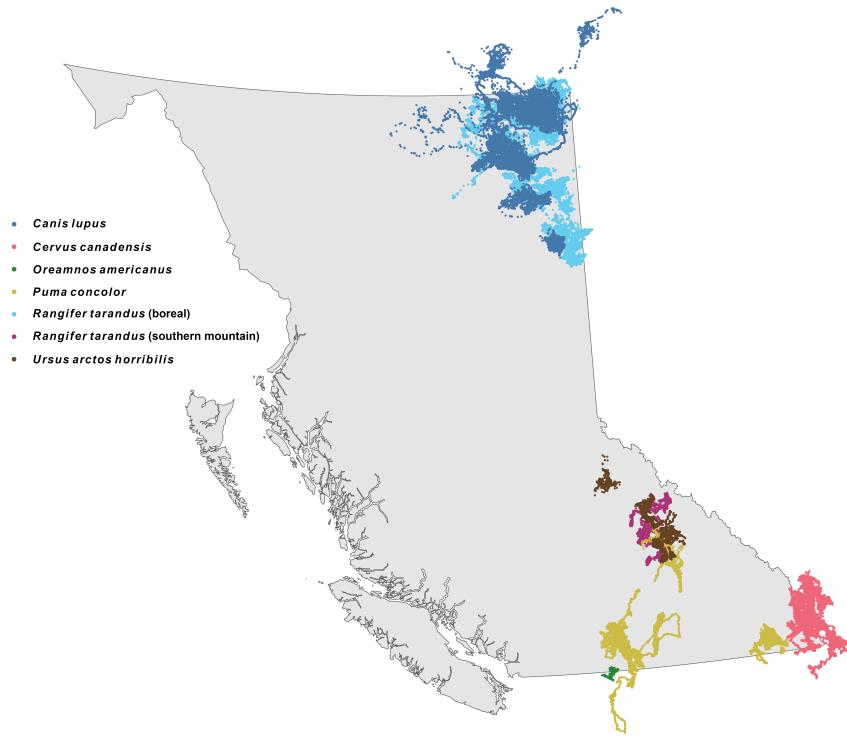


Figure 1: GPS telemetry data for the six species in this study.

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, and more details are available in appendices A (estimating how
84 temperature affects movement frequency and speed when moving), B (fitting Hierarchical
85 Resource Selection Functions), and C (simulating hourly temperature data to 2100 using the
86 four SSPs).

87 **2.1.1 GPS telemetry data**

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

⁹⁹ **2.1.2 Historical and projected temperature data**

¹⁰⁰ Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset
¹⁰¹ (Hersbach *et al.*, 2023) from the European Center for Medium-range Weather Forecasting
¹⁰² server (ECMWF; www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal tempera-
¹⁰³ ture was estimated for each location by extracting the value from the corresponding raster
¹⁰⁴ cell from the temporally nearest raster using the `extract()` function from the `terra` package
¹⁰⁵ (version 1.7-46, Hijmans, 2023) for `R` (R Core Team, 2024).

¹⁰⁶ We obtained rasters of projected monthly average temperature at a 0.08° resolution in BC
¹⁰⁷ from 2020 to 2100 under the different SSPs via the `climatenar` package (version 1.0, Burnett,
¹⁰⁸ 2023) for `R`. Since the climate projections only provided monthly means and ranges but no
¹⁰⁹ measures of variance or distributional assumptions, we used the hourly ERA5 data for BC
¹¹⁰ from 1998 to 2023 (extremes included, see Hersbach *et al.*, 2023) to calculate within-month
¹¹¹ variance in temperature, which we defined as the variance within a given pixel, month, and
¹¹² year. We then modeled the estimated variance using a GAM for location and scale (GAMLS,
¹¹³ see: Rigby & Stasinopoulos, 2005; Stasinopoulos & Rigby, 2007; section 7.9 in Wood, 2017).
¹¹⁴ The linear predictor for the location (i.e., the mean) included smooth terms of the within-
¹¹⁵ pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-
¹¹⁶ dimensional smooth of space, and a tensor interaction product term of space and month. The
¹¹⁷ linear predictor for the scale term (which governs the mean-variance relationship) included
¹¹⁸ smooth terms of the monthly mean, month, and space. We did not include a smooth of
¹¹⁹ year to avoid unrealistic projections when extrapolating beyond the range of historical data.
¹²⁰ Additional details are available in Appendix C.

¹²¹ We simulated hourly variation in weather by assuming temperature followed a normal
¹²² distribution with mean specified by the monthly `climatenar` climate projections and vari-
¹²³ ance as specified by the Gamma GAMLS. We then predicted changes in movement behavior
¹²⁴ and habitat selection as a function of the simulated temperature using the HGAMs and
¹²⁵ HRSFs. For each month within each year from 2020 to 2100, we simulated hourly weather

126 by including temperatures from the 0.1 to the 0.9 quantile by increments of 0.1, and we
127 weighted each quantile proportionally to the (normalized) Gaussian probability density for
128 each quantile (Appendix C).

129 **2.1.3 Resource rasters**

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

142 **2.2 Estimating mammals' instantaneous speeds**

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

149 Since `ctmm`'s movement models assume stochastic but non-zero speeds (i.e., a single,
150 stochastic moving state), data-informed speeds needed to be corrected so that the minimum

151 instantaneous speed could be 0. We performed this correction by subtracting each model's
152 mean speed while assuming speeds were χ^2 -distributed. The function we used is avail-
153 able on GitHub at [https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/
blob/main/functions/detrend_speeds.R](https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R). To avoid artifacts due to excessively small, non-
154 zero speeds, we determined whether an animal was moving or not using the inflection point
155 of each species' histogram of detrended speed estimates (Appendix A).
156

157 2.3 Estimating the effects of temperature on mammals' movement

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

163 2.3.1 Disentangling direct and indirect effects

164 In this manuscript, we separate the effects of temperature on mammalian movement into
165 indirect and direct effects. We call "indirect" all effects that can be intervened on by altering
166 an animal's habitat (its geographic space *sensu* Matthiopoulos, 2022), and we refer to all
167 other effects as "direct". For example, an increase in temperature may push an animal to
168 prefer higher forest cover in search of shade, and conservationists can thus mitigate these
169 indirect effects of temperature on movement behavior by increasing the availability of forested
170 areas, since the effect of temperature on movement is conditional on forest cover availability.

171 In contrast, the animal may avoid moving if temperatures are above 35°C, irrespective of
172 its geographic and environmental space (*sensu* Matthiopoulos, 2022), so it is not possible to
173 mitigate the effects of temperature on movement behavior (other than changing temperature
174 directly). We provide Directed Acyclical Graphs in Appendix A (modeling the effects of
175 temperature on movement rates), and Appendix B (modeling the effects of temperature on

176 habitat selection).

177 2.3.2 Effects of temperature on movement rates

178 We estimated the effects of temperature on mammals' movement state (moving or not) and
179 speed (when moving) using two Hierarchical Generalized Additive Models (HGAMs, see
180 Pedersen *et al.*, 2019 and the code chunk below) with the `mgcv` package for R (version 1.9-1,
181 Wood, 2017). The first HGAM estimated the probability that an animal was moving with
182 a binomial family of distributions and logit link function. The second HGAM estimated an
183 animal's speed (when moving) with a gamma family of distributions and log link function.
184 The HGAMs included random intercepts for each animal (`s(..., bs = 're')`), fixed-effect
185 intercepts for each species, and species-level `by` smooths for time of day, day of year, and
186 temperature (`s(..., by = species)`, see model I in Figure 4 of Pedersen *et al.*, 2019).
187 Additionally, the models had three tensor product interaction terms (`ti()`) for each species:
188 (1) day of year and time of day, (2) temperature and time of day, and (3) temperature and
189 day of year. These three terms accounted for: (1) seasonal changes in day length, (2) hourly
190 changes in the response to temperature (e.g., changes in nocturnality), and (3) seasonal
191 changes in the response to temperature (e.g., changes in coats and migration timing). The
192 HGAMs accounted for the cyclicity of time of day and day of year using cyclic cubic splines
193 (`bs = 'cc'`, Wood, 2017). Together, the binomial HGAM and the gamma HGAM inform
194 us on an animal's long-term average speed, since it is the product of the probability of
195 moving and its average speed when moving. We fit the models with fast REML ('`fREML`')
196 and discretized covariates (`discrete = TRUE`) to optimize computational efficiency with no
197 appreciable losses to model performance (Wood, Goude & Shaw, 2015; Wood *et al.*, 2017;
198 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)))

```

¹⁹⁹ 2.3.3 Effects of temperature on habitat selection

²⁰⁰ We estimated the effects of temperature on each species' selection for percent forest cover,
²⁰¹ elevation, and distance from water by fitting a Hierarchical Resource Selection Function for
²⁰² each species using an HGAM with a Poisson family of distributions and log link function (Ap-
²⁰³ pendix B, also see Aarts *et al.*, 2008). We accounted for the spatiotemporal autocorrelation
²⁰⁴ in the telemetry locations by weighting each point based on the telemetry's Autocorrelated
²⁰⁵ Kernel Density Estimate (Fleming & Calabrese, 2017; Noonan *et al.*, 2019b) to produce
²⁰⁶ estimates of second- and third-order habitat selection (*sensu* Johnson, 1980). While we rec-
²⁰⁷ ognize there are other important drivers of habitat selection (e.g., forest age, forest type,
²⁰⁸ prey availability), we decided to only use these three proxies to produce results that are
²⁰⁹ comparable between species and to make province-wide predictions simpler. Each species'
²¹⁰ 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)

```

211 Smooth effects of percent forest cover, elevation, and distance to water accounted for the
 212 species-level average selection strength for each resource. A random effect for each individ-
 213 ual animal corrected for uneven sampling across individuals, while factor smooth interaction
 214 terms (`bs = 'fs'`) accounted for individual-level resource selection (i.e., individual-level de-
 215 viations from the species-level average). Tensor interaction product terms (`ti()`) of the three
 216 resources and temperature estimated the change in resource selection at different tempera-
 217 tures. Finally, we included marginal smooth terms of temperature to account for species-
 218 and individual-level sampling biases over temperature (e.g., sampling more during warm pe-
 219 riods). Detections were weighted proportionally to their degree of independence from other
 220 temporally proximate detections (`weights = weight` – see Appendix B and Alston *et al.*,
 221 2022), while quadrature points had a weight of 1.

222 3 Results

223 Species differed in mean probabilities of movement (range: 0.05 – 0.3), mean speed when
 224 moving (range: 0.42 – 2.7 km/day), and mean distance traveled (range: 0.04 – 0.6 km/day),
 225 even after predicting for one-hour time intervals for all species (Table 2). Grizzly bears
 226 tended to move least often (probability of moving $P(M) \approx 0.05$), while wolves and pumas

227 moved most often ($P(M) \gtrsim 0.23$). When moving, mountain goats and southern mountain
228 caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.4$ m/s), while wolves had the highest mean speed
229 when moving ($\mathbb{E}(S|M) \approx 2.7$ m/s). Consequently, wolves traveled, on average, 50 km/day
230 – 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

231 At average temperatures, wolves preferred dense forest cover ($\gtrsim 50\%$) high elevations,
232 and distances from water < 10 km; elk preferred intermediate forest cover, elevations between
233 1 and 2 km, and distances from water of 5-15 km; mountain goats preferred sparse ($< 50\%$)
234 forest cover, elevations between 1 and 2 km; pumas preferred high forest cover, an elevation
235 of ~ 1 km, and distances from water < 10 km; boreal caribou selected for intermediate to high
236 forest cover, elevations near 500 m, and distances from water < 10 km; southern mountain
237 caribou selected for dense forest cover, elevations near 2 km, and distances from water $<$
238 5 km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and
239 distances from water < 2 km.

240 Including temperature in the models always increased within-sample prediction, but the
241 change was not always substantial (deviance explained increased between 0.2% and 18.6%,
242 with all HRSFs having an increase ≥ 4.6), and there was relatively strong agreement between

²⁴³ models with and without temperature (Fig. *SX pred vs pred*), but including temperature
²⁴⁴ resulted in substantially better fits for all models, especially HRSFs (all $\Delta\text{AIC} \leq -342$; Table
²⁴⁵ 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

²⁴⁶ 3.1 Effects of temperature on movement rates

²⁴⁷ The marginal effects of temperature varied in both direction and magnitude across species
²⁴⁸ (Fig. *AX*), even after accounting for differences in daily and seasonal activity (e.g., sleeping,
²⁴⁹ migration, hibernation; see Fig. *AX*). The smooths' credible intervals were generally quite
²⁵⁰ wide outside the typical temperature range of -20°C to 20°C , so the estimated trends were
²⁵¹ often not credible at the 95% level outside such range. Smooth interaction terms were well-
²⁵² behaved and indicated clear shifts in activity over time of day and day of year for all species.
²⁵³ The models explained reasonably high proportions of the deviance (10.7% for the binomial
²⁵⁴ model and 79.3% for the Gamma model) and had good in-sample prediction (Fig. *AX*).

255 All species' movement frequency and speed decreased with increasing sampling interval (Fig.
256 **AX**).

257 Most species adapted their daily and seasonal movement behavior to changes in temper-
258 ature (Fig. 2). Wolves, elk, pumas, and boreal caribou reduced their mid-day movement
259 rates when temperatures were above 20°C, and wolves, elk, and boreal caribou moved less on
260 summer days above 20°C. However, the precision of the estimated change depended on the
261 GPS sampling frequency (Fig. **AX**). While the `ctmm` models produced scale-independent
262 estimates of speed (i.e., model interpretation is independent of sampling time: Noonan *et al.*,
263 2019a), the accuracy, size, and stability of speed estimates still depended on the GPS sam-
264 pling frequency. This is because coarsely-sampled movement data contains information on
265 large-scale movements (e.g., range crossings, migrations) but not fine-scale movements (e.g.,
266 first-order habitat selection *sensu* Johnson, 1980). Using the boreal caribou as an example,
267 the 13-hour sampling interval allows us to reasonably estimate the caribou's movement path
268 at a temporal scale of approximately 13 hours (or greater), but we cannot produce reasonable
269 movement trajectories at a much finer (e.g., hourly) scale. Consequently, we suggest being
270 cautious when comparing estimated movement behaviors across species.

271 **3.2 Effects of temperature on habitat selection**

272 Species' relative selection strength (RSS) for resources depended on temperature, and
273 RSS was strongest for elevation and weakest for forest cover. Changes in RSS with tem-
274 perature were strongest for elevation and generally weakest for distance from water, but
275 there were no common trends across all species for any of the three resources. All species,
276 with the exception of pumas, exhibited a temperature-dependent shift in their preference
277 for forest cover. At higher temperatures, wolves, mountain goats, and grizzly bears be-
278 came less selective for forest cover, while elk and caribou became more selective. All species
279 shifted elevationally with temperature, although boreal caribou did not exhibit as strong of
280 a change. As temperatures rose, elk, mountain goats, cougars, and boreal caribou increased

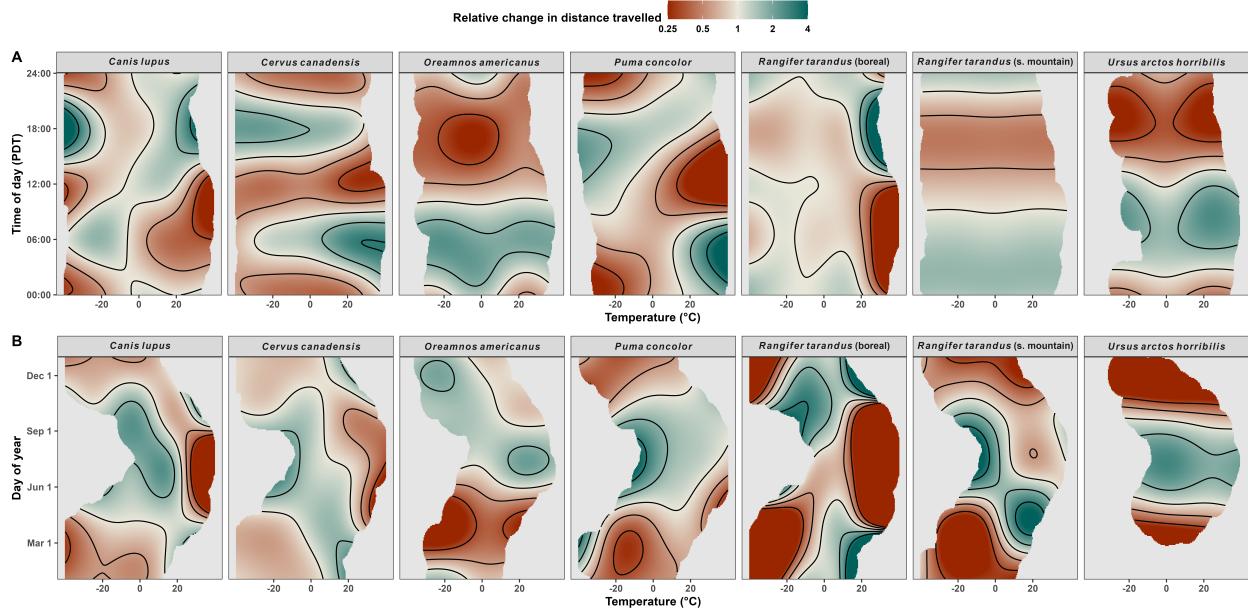


Figure 2: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day (**A**) and day of year (**B**). Predictions in 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^{±2}) for ease of readability.

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. **BX**).

3.3 Predicted changes in movement during the 21st century

The direction and magnitude of change in distance traveled varied greatly between species, but worse climate-change scenarios generally corresponded to greater absolute changes in behavior (Fig. 4). Under the best-case scenario, absolute projected changes by 2100 were small (approximately 0% to 2%), while absolute projected changes by 2100 ranged from ~1% (boreal caribou) to ~25% (southern mountain caribou) under the worst-case scenario. Boreal caribou and elk showed relatively little projected changes in yearly distance traveled. Throughout BC (Fig. 5), all species but elk and boreal caribou were expected to change their movement rates by 10 to 20% in 2100, relative to 2025, but the predicted changes varied spatially due to heterogeneity in climate change throughout the province. Across all

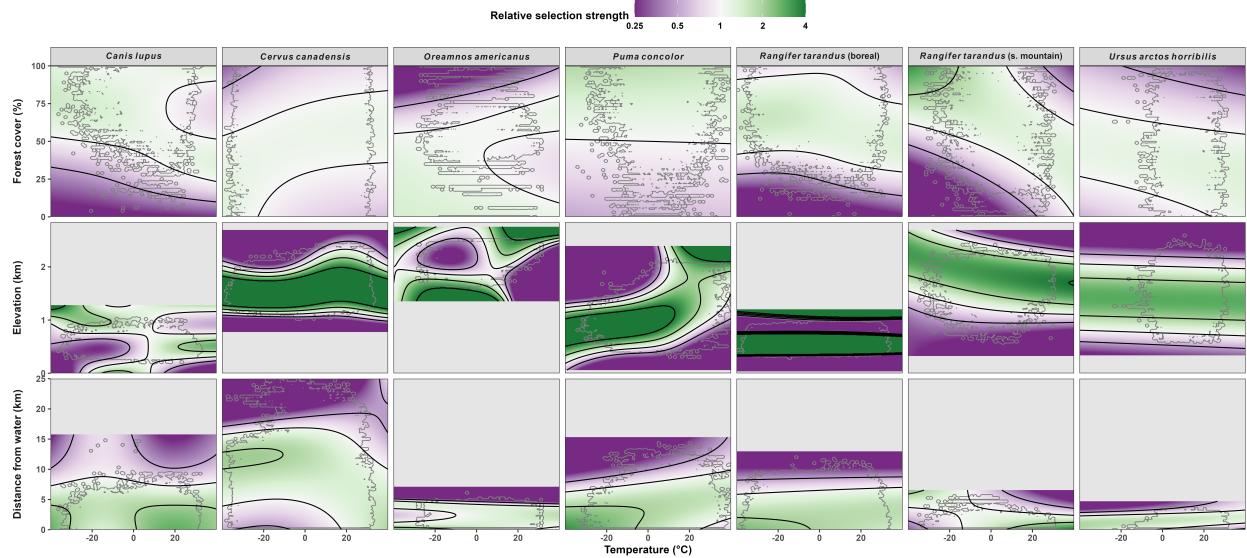


Figure 3: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were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

295 species, absolute changes were smallest under the best-case scenario and greatest under the
296 worst-case scenario.

307 All species were projected to reduce selection for their current range throughout the 21st
308 century, with the exception of grizzly bears, which showed little to no change under all four
309 the climate change scenario (@ref:fig(t-hrsfs)). The decreases in RSS were most evident in
310 the habitats with the top 5% RSS in the current range. Projected changes in the median-
311 RSS habitats were relatively small, but none increased throughout the century under any of
312 the climate change scenarios. As with distance traveled, the change in RSS in 2100 varied
313 throughout BC for all species (Fig. 7). All species were predicted to exhibit a decrease in
314 RSS throughout most of BC, with the exception of boreal caribou, which had a predicted
315 decrease in approximately 37% of the province, including their current range. While the
316 boreal caribou were expected to increase selection for altitudes > 1 km above sea level, the
317 estimated selection strength was highly uncertain and not credible at the 95% level (Fig.
318 **SX**).

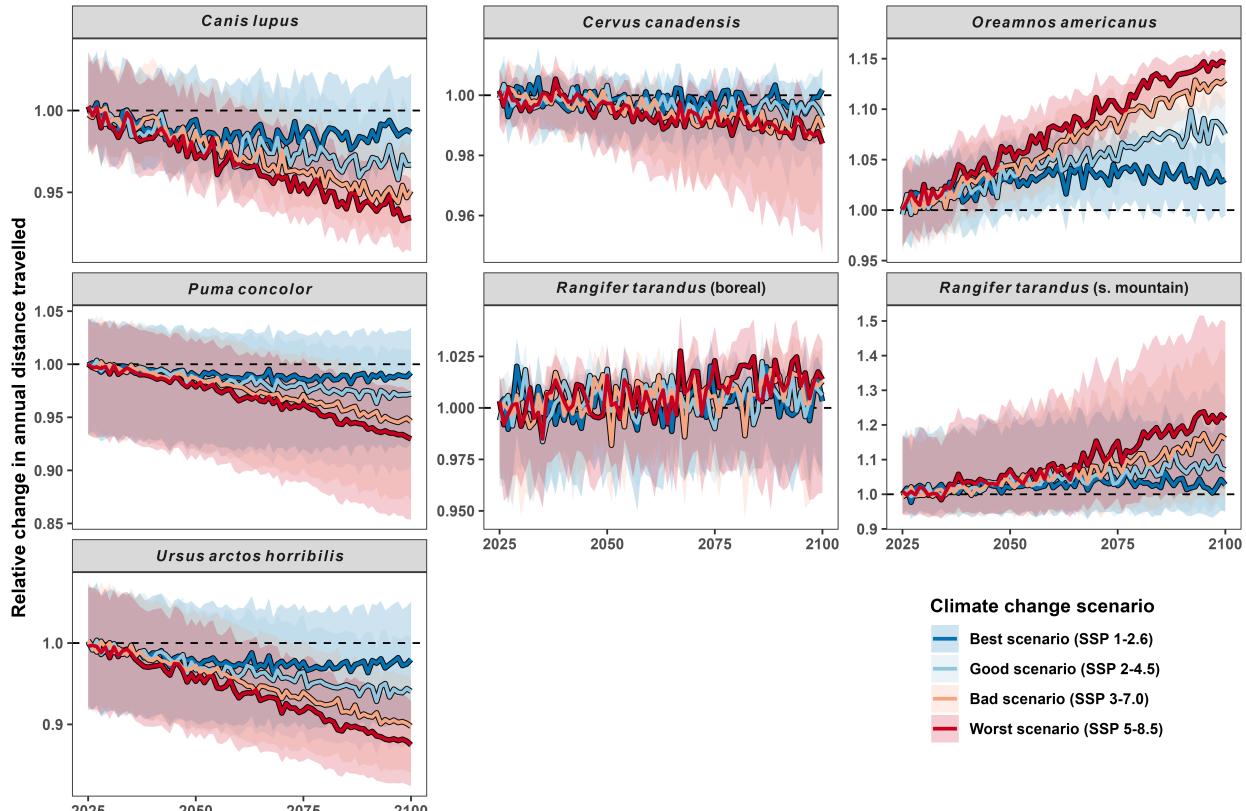


Figure 4: **The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios often result in the greatest change and greatest uncertainty.** Lines indicate the projected relative change in mean distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the average 95% Bayesian credible intervals for the area. 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.

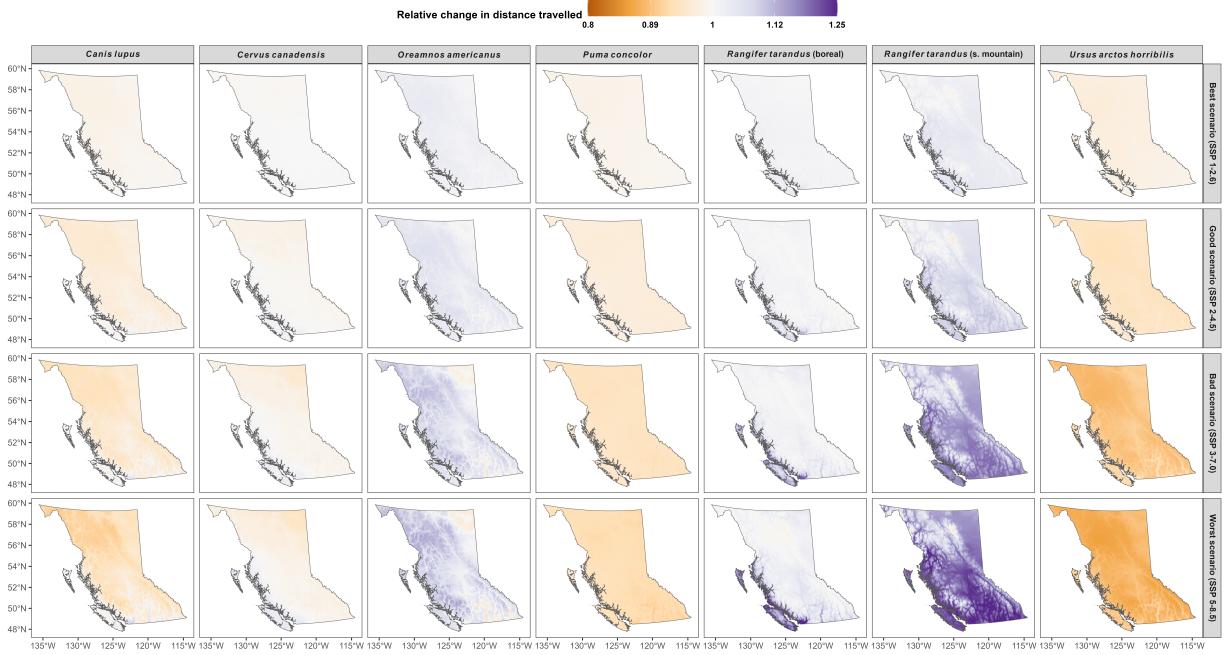


Figure 5: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, 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 ($\approx 2^{\pm 0.32}$; original data ranged 0.81 to 1.35). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest cover.

309 4 Discussion

310 We demonstrated that temperature is an important determinant of how and where mammals
 311 move, even while accounting for other seasonal drivers of movement (e.g., changes in pho-
 312 toperiod, hormones, and resources). Disentangling temperature from other drivers allows us
 313 to predict how changes in climate will affect mammalian movement even if all other drivers
 314 remain approximately constant or adapt at negligible rates. However, as habitats warm and
 315 animals are exposed to increasingly frequent extreme and novel conditions, our ability to
 316 confidently predict mammals' responses decreases. Predicting at the fringes of the surface
 317 plots we present comes with substantial uncertainty, particularly given that the responses are
 318 nonlinear. At unusually warm temperatures, mammals (and other homeotherms) overheat,
 319 so their movement behavior and that of their competitors, predators, and/or prey can often
 320 be substantially different from the behavior at typical temperatures. As extreme tempera-
 321 ture events become more frequent and prolonged (Yao *et al.*, 2022; Intergovernmental Panel

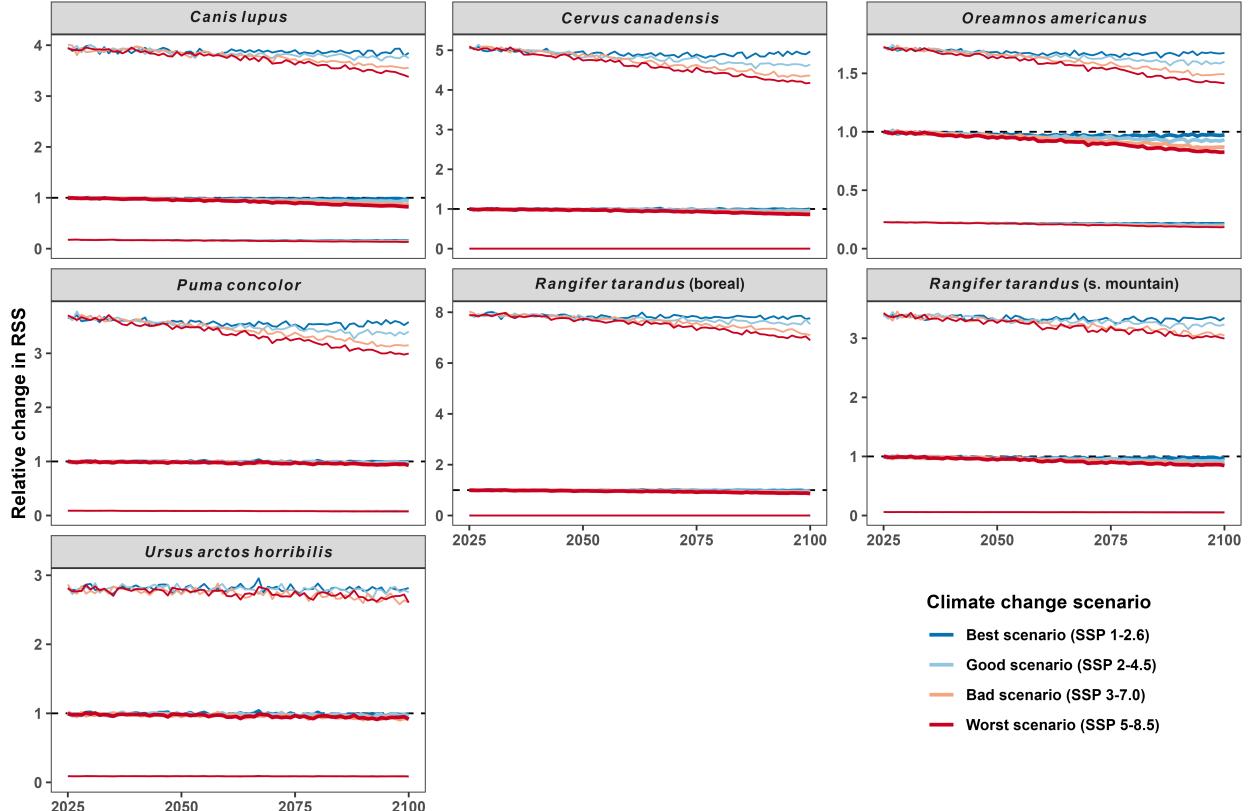


Figure 6: The intensity and direction of changes in habitat selection due to climate change vary among species, but no species are expected to exhibit an increase in relative selection strength (RSS). Lines indicate the projected change in RSS based on the 5th percentile (the worst 5%; bottom line), the median (the middle; bold), and 95% percentile (the best 5%; top line) habitats within the species' current extent. Changes are relative to the median RSS in 2025 across the four Shared Socioeconomic Pathways (SSPs).

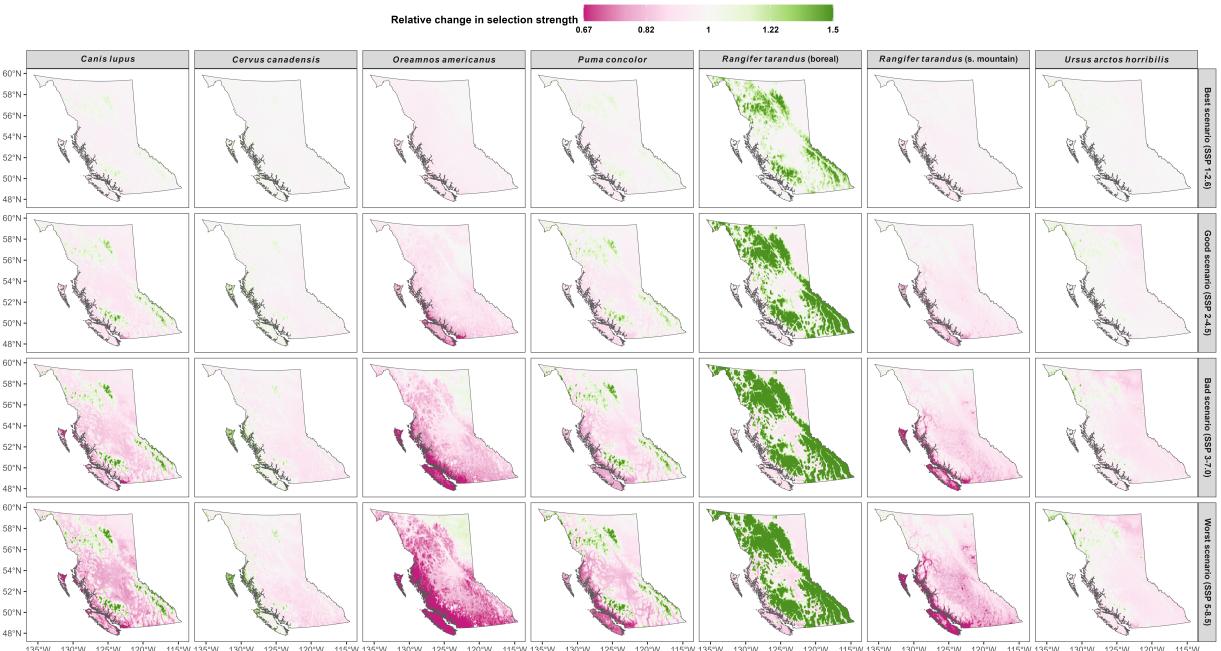


Figure 7: Climate change will impact each species' habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location's average RSS in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the log₂ 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).

322 On Climate Change, 2023), mammals will be increasingly forced to atypical behaviors, which
323 will have the potential to substantially alter community structures and behaviors, both dur-
324 ing such events and afterwards [Zhang *et al.* (2023);]. For instance, changes in climate
325 and phenology impact the life history and behavior of many hibernating mammals (Wells *et*
326 *al.*, 2022), but hot weather also affects mammals' sleep quality (e.g., wild boars, *Sus scrofa*:
327 Mortlock *et al.*, 2024) and likelihood to enter torpor (Australian eastern long-eared bat,
328 *Nyctophilus bifasciatus*: Fjelldal, Wright & Stawski, 2021). These changes can alter the frequency
329 and intensity of human-wildlife conflict, especially with the addition of growing pressures
330 from human development and presence (Sih *et al.*, 2011; Johnson *et al.*, 2018; Weststrate *et*
331 *al.*, 2024). At the same time, warmer winters may reduce mammals' energetic expenditure
332 (Berger *et al.*, 2018; Schmidt *et al.*, 2020), increase their ability to find food or be predated
333 upon (Gilbert *et al.*, 2017; Hou *et al.*, 2020; Pedersen *et al.*, 2021; Slatyer, Umbers & Arnold,
334 2022; Sullender *et al.*, 2023), and affect the timing and duration of migrations (Sawyer *et al.*,
335 2009; Xu *et al.*, 2021; Leclerc *et al.*, 2021) as well as the overall ease of movement as snow
336 cover and depth decrease (Leclerc *et al.*, 2021; Melin *et al.*, 2023). However, these changes
337 are likely to have complex consequences for population and ecosystem structures and dy-
338 namics as prey, predators, and prey experience altered and novel seasonal cycles. especially
339 given the increasingly common climate "weirding" (Bunnell *et al.*, 2011), which includes not
340 only warmer temperatures and more frequent and intense heat waves but also an increase in
341 various other extreme events (Yao *et al.*, 2022; Intergovernmental Panel On Climate Change,
342 2023), such as cold spells, floods and droughts, plant and animal die-offs and sudden growth
343 surges, and other changes in population dynamics and behaviors (sometimes referred to as
344 "black swan" events – see: Logares & Nuñez, 2012; Anderson *et al.*, 2017).

345 Our ability respond to current and future changes in climate is contingent on our ability
346 to prepare for and predict change. However, predicting animal behavior becomes increasingly
347 complicated as the conditions animals are exposed to deviate from current, typical condi-
348 tions, especially when responses are nonlinear. Consequently, we do not present our results

as a definitive guide to how mammals in BC will respond to climate change. Instead, we hope they serve as a starting point to (1) demonstrate that mammals' movement rates and habitat selection depend on temperature and (2) how one can estimate mammals' changes in movement behavior due to climate change. An important limitation of Figs. 2 and 3 is that we do not include measures of uncertainty around the estimated responses, as they cannot be incorporated easily in surface plots, and the purpose of the figures was to illustrate the magnitude and direction of the responses rather than contrasting the surfaces against some hypotheses. Still, we stress that uncertainty is crucial in producing transparent and informed results, particularly when using such estimates for decision-making or predicting future changes, as we do in Figs. 4 and 6. We present the spatial estimates of distance traveled and relative habitat selection strength in 2100 without measures of uncertainty for conciseness, but we suggest that future studies and reports include some form of compatibility intervals (Gelman & Greenland, 2019), whether these be Bayesian Credible intervals (McElreath, 2020) or Frequentist Confidence Intervals, although the latter do not provide a measure of uncertainty in the common sense of the word (Morey *et al.*, 2016; Amrhein, Greenland & McShane, 2019). As alternatives to heat-map surface plots, one may include compatibility intervals using faceted or perspective plots of the surfaces along with the intervals (e.g., Fig. 5 in Akkaya Hocagil *et al.*, 2024) or overlapping contour plots on the surfaces (e.g., Fig. 4.14 on page 187 of Wood, 2017). For a simpler figure, one could also include lines with compatibility intervals for the responses at different temperatures.

How to represent uncertainty may seem trivial to some, but communicating uncertainty is crucial in assessing risk probabilistically (Aven & Kvaløy, 2002; Ayre & Landis, 2012; Czado & Brechmann, 2014). Recent events in global politics, including global conflicts (McNutt & Hildebrand, 2022; Tollefson, 2022) and the rapid rise in generative machine learning (also referred to as artificial intelligence and GenAI, see Roumeliotis & Tsakikas, 2023; Van Noorden & Webb, 2023; DeepSeek-AI *et al.*, 2025) and its prohibitive energy and water demands (Li *et al.*, 2023) and carbon footprint (Luccioni, Viguier & Ligozat, 2024),

³⁷⁶ have placed doubt on the likelihood and feasibility of reaching climate change goals that
³⁷⁷ seemed achievable in the past decade (United Nations Environment Programme *et al.*, 2024).
³⁷⁸ Maintaining global warming below 1.5 or even 2.0°C has been questioned (United Nations
³⁷⁹ Environment Programme *et al.*, 2024), and mitigating climate change will require extensive
³⁸⁰ and widespread collaborative effort (e.g., Huang & Zhai, 2021). Similarly, protecting a third
³⁸¹ of the world's terrestrial and aquatic ecosystems (Section H, Targets 2 and 3 of Convention
³⁸² on Biological Diversity, 2022) appears less tangible as global political and environmental
³⁸³ conditions change rapidly and unpredictably (Sih *et al.*, 2011; Simmons, Nolte & McGowan,
³⁸⁴ 2021; Guenette, Kenworthy & Wheeler, 2022; Sovacool, Baum & Low, 2023), and achieving
³⁸⁵ such a goal will require active collaboration with local Peoples, especially Indigenous Peoples
³⁸⁶ (Wong *et al.*, 2020; Lamb *et al.*, 2023). Understanding the consequences of climate change on
³⁸⁷ mammals' movement behavior and spatial distribution (Williams & Blois, 2018) is a first step
³⁸⁸ towards anticipating and proactively responding to future changes in human-induced rapid
³⁸⁹ environmental change (Sih *et al.*, 2011), including climate change. In the following sections,
³⁹⁰ we discuss the implications of our results in more detail. We then expand on consequences
³⁹¹ for conservation during the 21st century and considerations for future studies.

³⁹² 4.1 Effects of temperature on movement rates

³⁹³ The lack of any common effects of temperature across all species' movement rates indicates
³⁹⁴ that the effects of climate change will vary across species and that responding to current
³⁹⁵ conditions and preparing for future changes will require a variety of adaptations as commu-
³⁹⁶ nities adapt and respond in complex and interconnected ways. Although our models do not
³⁹⁷ account for any physiological or explicit phenological changes (e.g., in the timing of sleep
³⁹⁸ and hibernation), the tensor product terms in Fig. 2 suggest that warmer temperatures
³⁹⁹ cause many species to alter their daily and seasonal activity patterns. For example, at cold
⁴⁰⁰ temperatures (-20°C), elk moved most in the early morning (6:00 PDT) and evening (18:00
⁴⁰¹ PDT), but they moved almost four times more at 6:00 PDT and half as much at 18:00 PDT

when temperatures were above 20°C. This suggests that while elk maintain a preference for crepuscular activity, they adapt their movement behavior to move more during warmer periods of the day (i.e., evening) on cold days and during cooler periods (i.e., early morning) on warmer days. The strong reduction in wolves', elk's, pumas', and boreal caribou's mid-day movement rates when temperatures are above 20°C suggests that the increasingly common and intense heat waves across British Columbia will often have community-wide impacts on movement rates, encounter rates (Martinez-Garcia *et al.*, 2020), and potentially community structure. More work is necessary on interspecific responses to temperature, including the effects of temperature on predation rates (Glass *et al.*, 2021; but see: Cunningham, Gardner & Martin, 2021; Brivio *et al.*, 2024). The increase in intensity and frequency of extreme heat events (Bunnell *et al.*, 2011; Yao *et al.*, 2022) will likely also impact the occurrence and timing of hibernation (Wells *et al.*, 2022) and migration or seasonal range expansions (Moryley, 2021; Malpeli, 2022; Carbeck *et al.*, 2022), not only as a direct effect of temperature, but also because of cascading changes in the availability and unpredictability of resources (Mezzini *et al.*, 2024).

The substantial increase in uncertainty around the estimated movement rates at temperatures below -20°C or above 20°C (Fig. A**X**) highlights the importance of including appropriate measures of uncertainty when evaluating the consequences of climate change on mammals' movement behavior. In this paper, we present our results cognizantly of the lack of uncertainty measures in many of our figures: We hoped to demonstrate how mammalian movement behavior depends on temperature while presenting the need for additional research. We expand on the importance of quantifying and communicating uncertainty in the last section of this discussion. Our relatively simple models indicate that changes in temperature will alter movement behavior even without accounting for large-scale physiological and behavioral adaptations, which may not be possible at the current rate of climate change (Heten *et al.*, 2014; Williams & Blois, 2018). Still, our models to indicate that some animals adapt their behavior phenology in response to temperature, as indicated by wolves', elk's,

⁴²⁹ caribou's, and grizzly bears' increased movement rates during warmer winters and spring
⁴³⁰ days.

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

⁴³² As with the effects of temperature on movement rates, the lack of common effects of
⁴³³ temperature across all species indicates that efficient and proactive habitat conservation
⁴³⁴ will require taxonomic nuance. In particular, our HRSFs do not account for any explicit
⁴³⁵ physiological responses to temperature that may impact movement such as changes in the
⁴³⁶ phenology of plants, ice, or mammalian physiology or behavior (e.g., seasonal coats, seasonal
⁴³⁷ migration) other than as direct responses to temperature. Consequently, the behavioral
⁴³⁸ changes we present should be interpreted carefully. While some seasonal cycles do not depend
⁴³⁹ directly on temperature and may thus not be impacted directly by climate change (such as
⁴⁴⁰ those driven by photoperiod, see Liu *et al.*, 2022), the predictions we present also rely on
⁴⁴¹ the assumption that mammals will not adapt these seasonal cycles based on temperature-
⁴⁴² dependent cues, such as weather (Xu & Si, 2019) or forage availability (Middleton *et al.*,
⁴⁴³ 2018). Additionally, it is important to stress the distinction between habitat selection and
⁴⁴⁴ quality. While animals tend to select for high-quality habitats (e.g., Wright, 2024), high
⁴⁴⁵ selection strength can also be a consequence of an ecological trap, an area animals are
⁴⁴⁶ attracted to that provides a net loss of fitness rather than a gain (Swearer *et al.*, 2021;
⁴⁴⁷ Zuñiga-Palacios *et al.*, 2021).

⁴⁴⁸ **4.3 Predicted changes in movement during the 21st century**

⁴⁴⁹ Achieving the goals laid out by the “30 by 30” conservation initiative (Section H, Targets
⁴⁵⁰ 2 and 3 of Convention on Biological Diversity, 2022) will require careful planning but often
⁴⁵¹ also rapid action. In the case of Canada, only 13.7% of its terrestrial areas and inland
⁴⁵² waters were protected at the end of 2023 (An act respecting transparency and accountability
⁴⁵³ in relation to certain commitments canada has made under the convention on biological

454 diversity, 2024; Environment and Climate Change Canada, 2024). Additionally, efficient
455 and effective conservation will require collaboration with Indigenous and local communities
456 to ensure Treaties are respected in the process (Turner & Clifton, 2009; Wong *et al.*, 2020;
457 e.g., Falardeau *et al.*, 2022; Lamb *et al.*, 2023) while also actively preparing for future change
458 (Desjardins, Friesen & Jordan, 2020; Hessami *et al.*, 2021). The large range in predicted
459 changes by 2100 (both across species and within species' current ranges) and high spatial
460 heterogeneity in figure 7 highlight the need for careful planning that incorporates not only
461 accurate estimates of change but also pragmatic and communicable measures of uncertainty
462 and variability around such estimates. The width of the averaged credible intervals in Figure
463 4 suggest that spatial and intra-individual variation should be accounted for when deciding
464 the location and size of protected areas.

465 The widespread decrease in RSS in for areas with ranges with the top 5% RSS underscores
466 the importance of moving beyond only using central estimates of change. While changes in
467 the median RSS over time are small to negligible (yet never positive), decreases in the top
468 5% are more accentuated. This perspective is particularly important in the case of habitat
469 selection modeling, since animals will be selecting most for (and thus spending more time in)
470 habitats with high RSS values, so changes in the upper extremes are more important than
471 changes in the median or lower extreme values. Similar arguments can be made for incorpo-
472 rating variation in temperature (including extreme events) when predicting future changes.
473 Estimating changes in future weather with monthly means alone is insufficient because a
474 change of 1-3 in mean monthly temperature may result in negligible predicted changes while
475 ignoring changes in the frequency and intensity of extreme temperatures (Bunnell *et al.*,
476 2011; Yao *et al.*, 2022; Zhang *et al.*, 2023).

477 Accurate estimates of the effects of changes in temperature on mammals' movement
478 require a holistic view of the direct effects of temperature on mammals' movement directly
479 as well as its effects on other drivers of movement, such as forage availability (Mezzini *et al.*,
480 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 (**need_ref?**), and food webs (**need_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).

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 address each consideration in the following three paragraphs.

Sampling schedules should be fine enough to reconstruct animals' movement at a sufficiently fine scale. Good estimates of an animal's speed and its movement path require

507 telemetry locations to be taken more often than the animal's directional persistence (Noo-
508 nan *et al.*, 2019a), so that, on average, the dataset contains multiple locations in between
509 changes in direction. What constitutes a change in direction depends on what movement
510 scale one is investigating. Small-scale movements and first-order spatial selection will re-
511 quire more frequent sampling than migratory movement or second- and third-order spatial
512 selection. While `ctmm` movement models are scale-invariant in that any model can be scaled
513 to larger or smaller areas and timescales, the model estimates are not independent of the
514 scale of the sampling frequency.

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

525 Quantifying and communicating uncertainty become particularly important as we predict
526 for conditions for which we have little to no data, such as during extreme events. Addition-
527 ally, estimating nonlinear trends is particularly difficult near the edges of the data (e.g.,
528 extremely high temperatures), especially when data is scarce. Consequently, the estimated
529 responses at the fringes of the surfaces in figures 2 and 3 are more likely likely to be poorly
530 estimated, particularly in the case of HRSFs, but increasing data density throughout the
531 resource-temperature surfaces can ameliorate the issue. Preparing for future changes re-
532 quires some degree of inevitable risk, so it is imperative that models be statistically sound
533 and interpretable, and that results are communicated transparently and clearly to decision

⁵³⁴ makers and the public alike.

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