

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 behaviour, 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.

¹ 1 Introduction

² For most animals, movement is a rapid and low-cost response to a variety of stimuli [1].
³ Animals move to maximize resource availability [e.g., food, water, shelter, see: 2,3], optimize
⁴ habitat use [4], and escape predation [5–7]. However, ambient temperature affects mammals'
⁵ movement rates by altering the energetic cost of movement [8–12], the ease of movement
⁶ [e.g., snow depth and density, see 13,14,15], and the risk of overheating [16,17]. Animals
⁷ may search for a short-term buffer from extreme heat or cold via thermal refugia [18–22],
⁸ which may even be preferred over forage abundance [e.g., 23]. Additionally, temperature also
⁹ affects movement indirectly through other drivers of movement behaviour, such as trophic
¹⁰ interactions [24]. Changes in temperature thus affects how animals move [e.g., movement
¹¹ frequency and speed – their movement behaviour: 1,17] and where they move to [i.e., their
¹² habitat selection: 25,26,27].

¹³ Temperature also affects the consequences of animal movement, such as encounter rates
¹⁴ with resources [28], other animals [29], and humans [30], and these changes are exacerbated
¹⁵ at extreme temperatures [27,31,32]. But what counts as “extreme” varies across species:
¹⁶ thermal specialists are more sensitive to small changes outside their typical range [e.g., 27],
¹⁷ while thermal generalists can adapt more easily to change [33]. However, generalists’ greater
¹⁸ adaptability is tested when they are subject to changes that are more severe [34], affect
¹⁹ many factors [e.g., temperature, phenology, and resource availability: 35], or are too rapid
²⁰ to respond within the span of a lifetime or a few generations [11,36,37].

²¹ In the last 200 years, many ecosystems experienced widespread warming that resulted
²² in milder and shorter winters, hotter and longer summers, and a greater risk of extremely
²³ high temperatures and severe forest fires [38,39]. Over the next 100 years, these changes
²⁴ are expected to worsen and continue to impact mammals’ fitness, movement behaviour,
²⁵ and habitat selection as animals cope with growing heat stress [40,41] and more frequent
²⁶ and intense extreme events [42], along with increasing anthropogenic pressure [30,43,44].

27 Consequently, it remains unclear how or whether species will be able to respond to climate
28 change in the current century [40,41,45], especially when populations fail to adapt to changes
29 [46,47] or are physiologically incapable to do so [48,49]. Uncertainty in future conditions and
30 their consequences on ecosystems present a need for a comprehensive understanding of (1)
31 the direct effects of temperature on animal movement behaviour and (2) the implications this
32 will have on populations and species' adaptability and resiliency, community structure, and
33 biodiversity at large. Recent work has documented the effects of climate change on mammals'
34 ranges [14], movement behaviour [15], thermoregulation [50], and trait-based responses [34],
35 but it is still unclear how mammals will adapt their small-scale movement and habitat
36 selection to changes in temperature during the 21st century [38,4, but see 16].

37 Understanding the direct and indirect impacts of temperature on mammalian movement
38 is essential for decision makers to be able to prepare for and respond to change in a proactive
39 manner [34, e.g., 44]. The Canadian province of British Columbia is currently experiencing
40 rapid widespread warming [51,52], phenological shifts [e.g., 53,54], and more frequent and
41 intense extreme events [e.g., 55], including forest fires [39]. As we approach the deadline for
42 the “30 by 30” conservation initiative, a global effort to conserve 30% of the world’s lands
43 and oceans by 2030 [Section H, Targets 2 and 3 of 56], decision makers must understand
44 which areas will be of greatest value for maximizing the project’s effectiveness. Predicting
45 how climate change will affect how, when, and where animals will move is necessary for
46 identifying which landscapes are most valuable now as well as in the future. Failing to
47 understand how changes in temperature will affect mammalian movement behaviour and
48 habitat selection will hinder our ability to respond to the current climate crisis and make
49 decisions that are viable in the long term.

50 This paper provides an analysis of the effects of air temperature on the movement of
51 six terrestrial mammal species in British Columbia (BC), Canada (*Canis lupus*, *Cervus*
52 *canadensis*, *Oreamnos americanus*, *Puma concolor*, boreal and southern mountain *Rangifer*
53 *tarandus*, and *Ursus arctos horribilis*; Table 1). Using over 25 years of telemetry data

54 throughout a large spatial range of British Columbia and hourly air temperature data, we
 55 estimate how mammals altered their probability of movement, speed when moving, and
 56 habitat selection in response to temperature. We then pair the estimated responses with
 57 climate change projections to forecast the species' movement during the 21st century under
 58 different climate-change scenarios [referred to as Shared Socioeconomic Pathways, SSPs – see
 59 57]. We disentangle the direct and indirect effects of temperature on the movement behaviour
 60 of terrestrial mammals and discuss the consequences of these changes at the individual,
 61 population, and landscape levels.

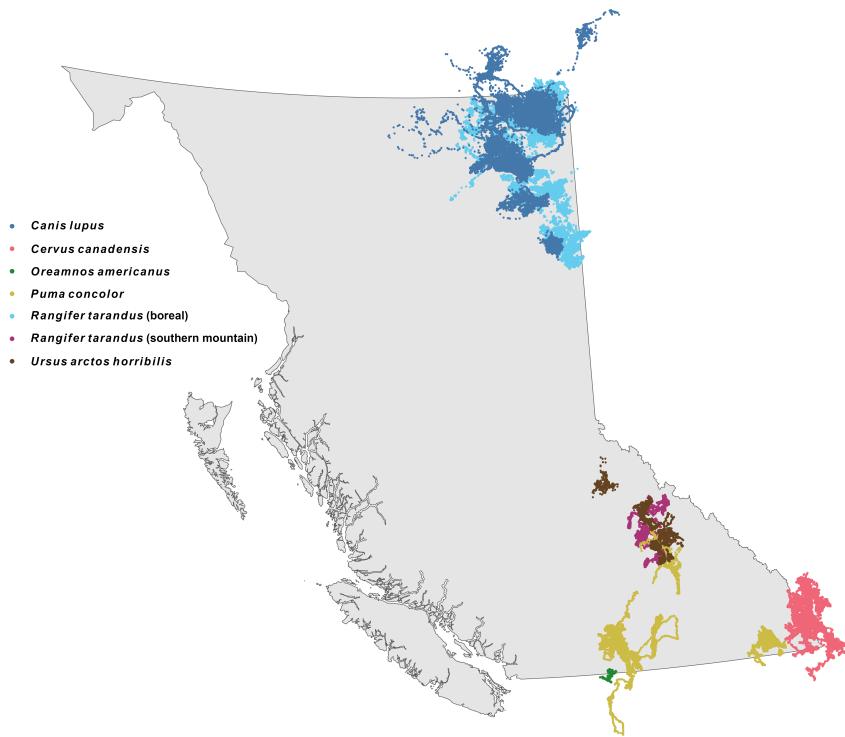


Figure 1: GPS telemetry data for the six species in this study.

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 resolved speed (Has speed) for each of the species in this study.

Species	Start	End	Δt (hours)	Animals	Has speed
<i>Canis lupus</i>	2013-01-27	2017-08-29	0.25	39	39
<i>Cervus canadensis</i>	2007-01-13	2013-11-20	2.00	169	169

Species	Start	End	Δt (hours)	Animals	Has speed
<i>Oreamnos americanus</i>	2019-06-25	2023-10-05	6.25	11	10
<i>Puma concolor</i>	2006-02-05	2021-07-13	2.00	29	29
<i>Rangifer tarandus</i> (boreal)	2011-03-02	2018-01-04	13.00	146	131
<i>Rangifer tarandus</i> (s. mountain)	1998-03-21	2009-06-07	6.00	22	20
<i>Ursus arctos horribilis</i>	2004-09-30	2009-09-07	1.00	18	18

62 2 Methods

63 2.1 Datasets used

64 This study leverages four main datasets: (1) a multi-species collection of GPS telemetry
 65 data (Fig. 1); (2) historical hourly reanalyzed air temperature from the ERA5 dataset from
 66 the European Center for Medium-range Weather Forecasting; (3) resource rasters of percent
 67 forest cover, elevation, and distance from water; and (4) climate change projections under
 68 four Shared Socioeconomic Pathways [SSPs, see 57]. We detail the data sources and analyses
 69 in the sections below.

70 2.1.1 GPS telemetry data

71 Elk (*Cervus canadensis*) data from [58] were downloaded from Movebank [study name: Elk
 72 in southwestern Alberta, see 59], while boreal caribou (*Rangifer tarandus*) and wolf (*Canis*
 73 *lupus*) telemtries were acquired via a public BC Oil and Gas Research and Innovation So-
 74 ciety repository (<https://www.bcgoris.ca/projects/boreal-caribou-telemetry-data>). **MISS-**

75 **ING INFO ON OTHER TELEMETRY DATA.** From the full set of telemetry data,
 76 a total of 2396 GPS locations (0.16%, including collar calibration data) were removed us-
 77 ing diagnostic plots of (1) distance from the median location, (2) straight-line displacement
 78 between locations, (3) turning angle, and (4) time interval between consecutive points. Par-
 79 ticular attention was paid to points with large turning angles ($\gtrapprox 170^\circ$) and excessively high

80 straight-line displacement, especially if antecedent and subsequent points indicated station-
81 ary behaviour. See Appendix A for additional information.

82 **2.1.2 Historical and projected temperature data**

83 Rasters of hourly reanalyzed air temperature data were downloaded from the ERA5 dataset
84 [60] from the European Center for Medium-range Weather Forecasting server (ECMWF;
85 www.ecmwf.int; <https://cds.climate.copernicus.eu>). Proximal temperature was estimated
86 for each location by extracting the value from the corresponding raster cell from the tempo-
87 rally nearest raster using the `extract()` function from the `terra` package [version 1.7-46,
88 61] for `R` [62].

89 We obtained rasters of projected monthly average temperature at a 0.08° resolution in BC
90 from 2020 to 2100 under the different SSPs via the `climatenetR` package [version 1.0, 63] for
91 `R`. Since the climate projections only provided monthly means and ranges but no measures of
92 variance or distributional assumptions, we used the hourly ERA5 data for BC from 1998 to
93 2023 [extremes included, see 60] to calculate within-month variance in temperature, which
94 we defined as the variance within a given pixel, month, and year. We then modeled the
95 estimated variance using a GAM for location and scale [GAMLS, see: 64,65,section 7.9 in 66].
96 The linear predictor for the location (i.e., the mean) included smooth terms of the within-
97 pixel monthly mean temperature (within each year), month (as a cyclic smooth), a two-
98 dimensional smooth of space, and a tensor interaction product term of space and month. The
99 linear predictor for the scale term (which governs the mean-variance relationship) included
100 smooth terms of the monthly mean, month, and space. We did not include a smooth of year
101 to avoid unrealistic projections when extrapolating beyond the range of historical data.

102 We simulated hourly variation in future weather by assuming hourly temperature followed
103 a normal distribution with mean specified by the monthly `climatenetR` climate projections
104 and variance as specified by the Gamma GAMLS. We then predicted changes in movement
105 behaviour and habitat selection as a function of the simulated temperature using the HGAMs

106 and HRSFs. For each month within each year from 2020 to 2100, we simulated hourly
107 weather by including temperatures from the 0.1 to the 0.9 quantile by increments of 0.1, and
108 we weighted each quantile proportionally to the (normalized) Gaussian probability density
109 for each quantile.

110 2.1.3 Resource rasters

111 We estimated percent forest cover and distance from water using the rasters created by
112 [67]. We calculated total forest cover by summing the temporally static rasters of ever-
113 green/deciduous needle-leaf trees, evergreen broadleaf trees, deciduous broadleaf trees, and
114 mixed/other trees (raster classes 1-4, respectively). We converted the raster of percent cover
115 of open water (class 12) to a binary raster of pixels with water (cover > 0%) or without water
116 (cover = 0%) and then calculated each pixel's distance from the nearest pixel with water
117 using the `distance()` function from the `terra` package. Finally, we obtained two digital
118 elevation models using the `get_elev_raster()` function from the `elevatr` package [version
119 0.99.0, 68]: We used a raster with a zoom of 6 (0.009°) for model fitting and one with a zoom
120 of 3 (0.08°) for downloading climate change projections via `climatenar`. All final rasters and
121 code are available on GitHub at <https://github.com/QuantitativeEcologyLab/bc-mammals-temperature>.

123 2.2 Estimating mammals' instantaneous speeds

124 We modeled each animal's movement using continuous-time movement models [69] via the
125 `ctmm` package [version 1.2.0, 70] for R. We then estimated mammals' instantaneous speeds
126 by applying the `ctmm::speeds()` function on all models with finite speed estimates [415 of
127 433, see 69,71]. The 18 animals with insufficiently fine sampling were for one mountain goat,
128 15 boreal caribou, and 2 southern mountain caribou (Table 1).

129 Since ‘ctmm’s movement models assume stochastic but non-zero speeds (i.e., a sin-
130 gle, stochastic moving state), data-informed speeds needed to be corrected so that the

minimum instantaneous speed could be 0. We performed this correction by subtracting each model's mean speed while assuming speeds were χ^2 -distributed. The function we used is available on GitHub at https://github.com/QuantitativeEcologyLab/bc-mammals-temperature/blob/main/functions/detrend_speeds.R. To avoid artifacts due to excessively small, non-zero speeds, we determined whether an animal was moving or not using the inflection point of each species' histogram of detrended speed estimates, as k -nearest neighbors did not discriminate between states well (Fig. S3).

2.3 Estimating the effects of temperature on mammals' movement

The following sections detail the statistical framework and modelling we used to estimate the effect on temperature on mammals' movement. To assess the importance of including temperature as an explicit covariate (rather than including its effects with time of day and day of year), we fit models with and without smooth effects of temperature and compared the deviance explained, model predictions, and AIC values of the two sets of models. We provide the relevant Directed Acyclical Graphs in the Appendix (Figs. S1-S2).

2.3.1 Disentangling direct and indirect effects

In this study, we separate the effects of temperature on mammalian movement into indirect and direct effects. We call "indirect" all effects that can be intervened on by altering an animal's habitat [*its geographic space sensu* 72], and we refer to all other effects as "direct". For example, an increase in temperature may push an animal to prefer higher forest cover in search of shade, and conservationists can thus mitigate these indirect effects of temperature on movement behaviour by increasing the availability of forested areas, since the effect of temperature on movement is conditional on forest cover availability. In contrast, the animal may avoid moving if temperatures are above 35°C, irrespective of its geographic and environmental space [*sensu* 72], so it is not possible to mitigate the effects of temperature on movement behaviour (other than changing temperature directly). We provide the relevant

156 Directed Acyclical Graphs in the Appendix (Figs. S1-S2).

157 **2.3.2 Effects of temperature on movement rates**

158 We estimated the effects of temperature ($^{\circ}\text{C}$) on mammals' movement state (moving or
159 not) and speed when moving using two Hierarchical Generalized Additive Models [HGAMs,
160 see 73 and the code chunk below] with the `mgcv` package for R [version 1.9-1, 66]. The
161 first HGAM estimated the probability that an animal was moving, $P(M)$, with a binomial
162 family of distributions and logit link function. The response variable `moving` was coded as
163 1 if moving and 0 if not. The second HGAM estimated an animal's speed when moving
164 (`speed`) with a gamma family of distributions and log link function. The HGAMs included
165 random intercepts for each animal (`s(animal, bs = 're')`), fixed-effect intercepts for each
166 species (`species`), and species-level `by` smooths (`s(..., by = species)`), which allowed
167 each species' term to be estimated independent of other species [see model I in Figure 4
168 of 73]. The `by` smooths accounted for trends in time of day (in Pacific Daylight Time;
169 `tod_pdt`), day of year (`doy`), and temperature (`temp_c`). Additionally, the models had
170 three tensor product interaction terms (`ti()`) by each species: (1) day of year and time
171 of day, (2) temperature and time of day, and (3) temperature and day of year. These
172 three terms accounted for: (1) seasonal changes in day length, (2) hourly changes in the
173 response to temperature (e.g., changes in nocturnality), and (3) seasonal changes in the
174 response to temperature (e.g., changes in coats and migration timing). Finally, smooth
175 terms of log-transformed hours between GPS locations (`dt`) accounted for irregular sampling
176 rates. A global term of `log(dt)` accounted for the overall effect of sampling interval, while
177 a factor-smooth interaction term (`s(log(dt), species, bs = 'fs')`) allowed for species-
178 level deviations from the global term while assuming a common smoothness parameter across
179 species [see model GS in Figure 4 of 73]. The HGAMs accounted for the cyclicity of time of
180 day and day of year using cyclic cubic splines [`bs = 'cc'`; see p. 202 of 66]. Together, the
181 binomial HGAM and the gamma HGAM inform us on an animal's long-term average speed,

182 since it is the product of the probability of moving and its average speed when moving. We fit
 183 the models with fast Restricted Maximum Likelihood ('fREML') and discretized covariates
 184 (`discrete = TRUE`) to optimize computational efficiency with no appreciable losses to model
 185 performance [74–76]. Additional details are provided in Appendix B.

```
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)))
```

186 2.3.3 Effects of temperature on habitat selection

187 We estimated the effects of temperature on each species' selection for percent forest cover
 188 (`forest_perc`), elevation (`elevation_m`), and distance from water (`dist_water_m`) by fit-
 189 ting a Hierarchical Resource Selection Function for each species using an HGAM with a
 190 Poisson family of distributions and log link function [Appendix B, also see 77]. We ac-
 191 counted for the spatiotemporal autocorrelation in the telemetry locations by weighting each
 192 point based on the telemetry's Autocorrelated Kernel Density Estimate [78,79] to produce es-
 193 timates of second- and third-order habitat selection [*sensu* 80]. While we recognize there are

194 other important drivers of habitat selection (e.g., forest age, forest type, prey availability),
 195 we decided to only use these three proxies to produce results that are comparable between
 196 species and to make province-wide predictions simpler. Each species' model had the same
 197 structure:

```

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

198 Smooth effects of percent forest cover, elevation, and distance to water accounted for
 199 the species-level average selection strength for each resource. A random effect for each in-
 200 dividual animal (`s(animal, bs = 're')`) corrected for uneven sampling across individuals,
 201 while factor smooth interaction terms (`bs = 'fs'`) accounted for individual-level resource
 202 selection (i.e., individual-level deviations from the species-level average). Tensor interaction
 203 product terms (`ti()`) of the three resources and temperature estimated the change in re-
 204 source selection at different temperatures. Finally, we included marginal smooth terms of
 205 temperature to account for species- and individual-level sampling biases over temperature
 206 (e.g., sampling more during warm periods). Detections were weighted proportionally to their
 207 degree of independence from other temporally proximate detections [`weights = weight` –
 208 see Appendix B and 81], while quadrature points had a weight of 1. Quadrature points were
 209 obtained using all raster cells in the 99.9% AKDE percentile. The number of quadrature
 210 locations greatly outnumbered the number of observed locations (Fig. S13), especially after

211 accounting for weighting based on the degree of autocorrelation and the number of home
212 range crossings (Fig. S14).

213 3 Results

214 Data were relatively scarce for temperatures lower than -20°C or above 20°C (Fig. S4).
215 Species differed in overall mean probabilities of movement (range: 0.05 – 0.3), mean speed
216 when moving (range: 0.42 – 2.7 km/day), and mean distance traveled (range: 0.04 – 0.6
217 km/day; Table 2). Grizzly bears tended to move least often (probability of moving $P(M) \approx$
218 0.05), while wolves and pumas moved most often ($P(M) \gtrapprox 0.23$). When moving, mountain
219 goats and southern mountain caribou moved the slowest ($\mathbb{E}(S|M) \approx 0.4 \text{ m/s}$), while wolves
220 had the highest mean speed when moving ($\mathbb{E}(S|M) \approx 2.7 \text{ m/s}$). Consequently, wolves
221 traveled, on average, 50 km/day – 2.5 to 16.7 times further than other mammals.

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

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

222 Near 0°C , wolves preferred dense forest cover ($\gtrapprox 50\%$) high elevations, and distances
223 from water $< 10 \text{ km}$; elk preferred intermediate forest cover, elevations between 1 and 2 km,
224 and distances from water of 5–15 km; mountain goats preferred sparse (< 50%) forest cover,
225 elevations between 1 and 2 km; pumas preferred high forest cover, an elevation of $\sim 1 \text{ km}$,
226 and distances from water $< 10 \text{ km}$; boreal caribou selected for intermediate to high forest

cover, elevations near 500 m, and distances from water < 10 km; southern mountain caribou selected for dense forest cover, elevations near 2 km, and distances from water < 5 km; and grizzly bears selected for sparse forest cover (25-50%), elevation near 1 km, and distances from water < 2 km.

Including temperature in the models always increased within-sample prediction, but the change was not always substantial (deviance explained increased between +0.2% and +18.6%, with all HRSFs having an increase $\geq +4.6\%$), and there was relatively strong agreement between models with and without temperature (Figs. S5 and S13), but including temperature resulted in substantially lower AIC values for all models, especially HRSFs (all $\Delta\text{AIC} \geq 342$; Table 3). Although this can be interpreted as evidence for a better fit, it is important to note that the addition of terms generally decreases AIC when sample sizes are large, even if the more complex model is not closer to the true model [see section 1.8.6, pages 52-54 of 66].

Table 3: Changes in deviance explained (ΔDE) and Akaike Information Criterion (ΔAIC) from including temperature in the models estimating probability of movement ($P(M)$) and speed when moving (Speed) as well as in species-level Hierarchical Resource Selection Functions (HRSF). Unlike conventional marginal AIC [82], The AIC values provided by the `mrgcv` package for R are calculated using the models' estimated effective degrees of freedom and the Bayesian variance-covariance matrices, which avoids issues related to random effects or Restricted Maximum Likelihood (REML).

Model	Species	ΔDE	ΔAIC
$P(M)$	All	0.5%	5927
Speed	All	0.2%	1682
HRSF	<i>Canis lupus</i>	9.2%	6566
HRSF	<i>Cervus canadensis</i>	4.6%	4448
HRSF	<i>Oreamnos americanus</i>	18.6%	813
HRSF	<i>Puma concolor</i>	8%	966
HRSF	<i>Rangifer tarandus</i> (boreal)	5.3%	5637

Model	Species	ΔDE	ΔAIC
HRSF	Rangifer tarandus (s. mountain)	12%	342
HRSF	Ursus arctos horribilis	17.7%	914

240 3.1 Effects of temperature on movement rates

241 The effects of temperature on movement rates varied in both direction and magnitude across
 242 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,
 243 migration, hibernation; see Figs. S6-S8). Smooth interaction terms were well-behaved and
 244 indicated clear shifts in activity over time of day and day of year for all species. The models
 245 explained reasonably high proportions of the deviance (10.7% for the binomial model and
 246 79.3% for the Gamma model) and had good in-sample prediction (Fig. S9). All species
 247 adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 2).
 248 For example, wolves, elk, pumas, and boreal caribou reduced their mid-day and summer
 249 movement rates when temperatures were above 20°C. However, uncertainties around the
 250 estimated effects were often higher at extreme temperatures due to data scarcity. All species'
 251 estimated probability of moving decreased with sampling intervals approximately above 1
 252 hour, and most species' estimated speed when moving decreased monotonically with sampling
 253 interval, although the estimated trends were highly uncertain for some species (Fig. S10).

254 3.2 Effects of temperature on habitat selection

255 Species' relative selection strength (RSS) was generally strongest for elevation and weakest
 256 for forest cover, but species' RSS for resources depended on temperature. Changes in
 257 RSS with temperature were also strongest for elevation and generally weakest distance from
 258 water, but there were no common trends across all species for any of the three resources.
 259 All species, with the exception of pumas, exhibited a clear temperature-dependent shift
 260 in their preference for forest cover. At higher temperatures, wolves, mountain goats, and

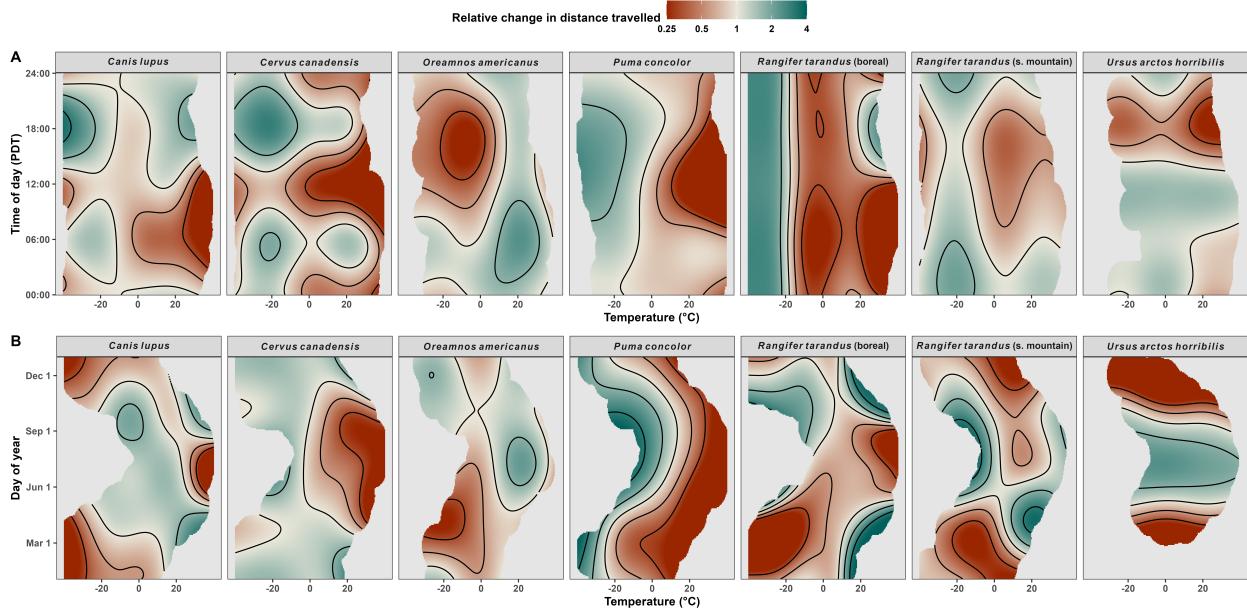


Figure 2: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT (**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 $2^{\pm 2}$ for ease of readability.

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

269 3.3 Predicted changes in movement during the 21st century

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

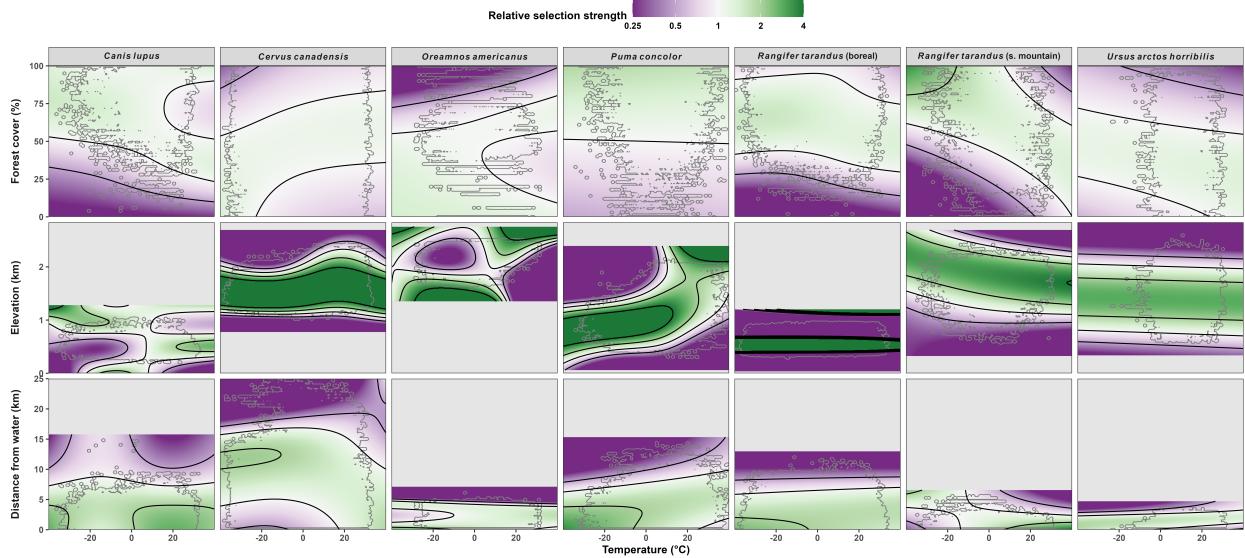


Figure 3: Temperature strongly affects mammals' habitat selection. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were re-centered 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 (6). 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 increase in approximately 67% of the province, including their current range. The increase was in great part due to the estimated increase in selection for high-elevation areas that are well outside the population's current range.

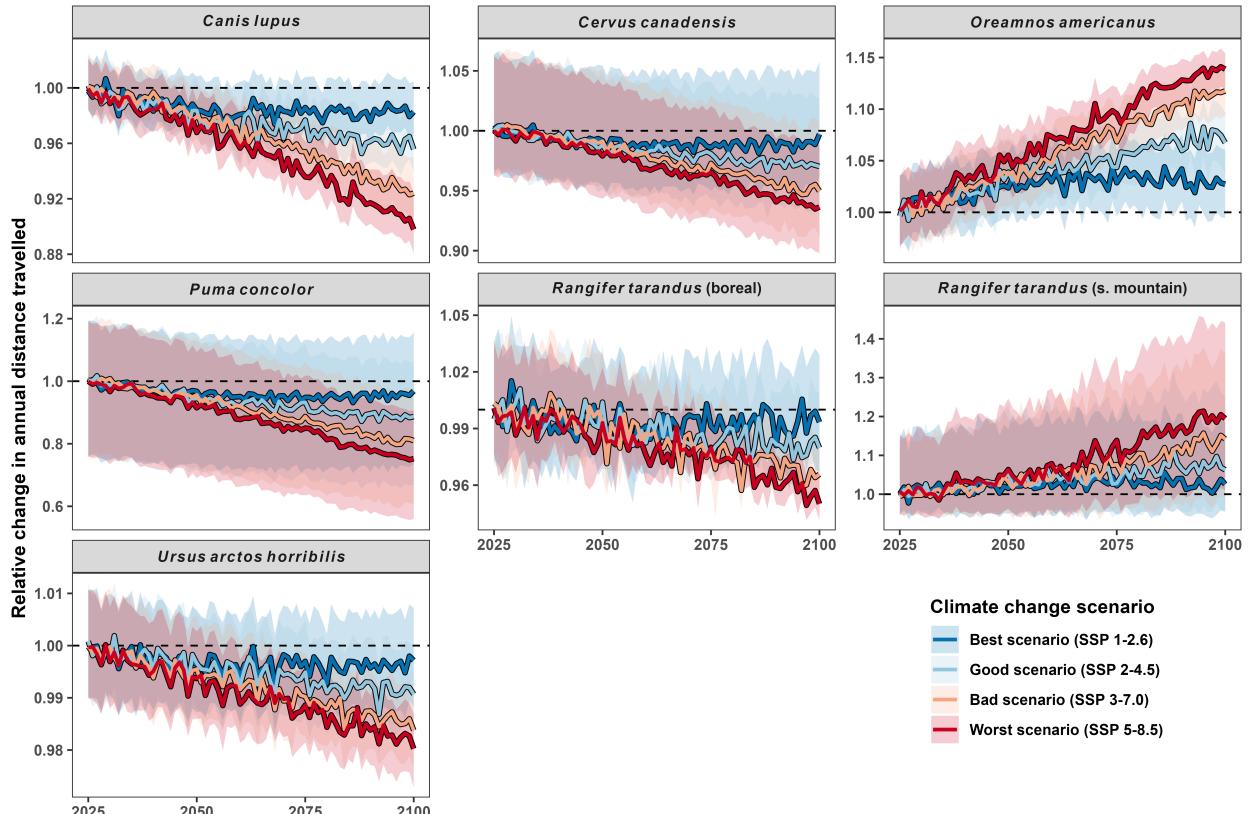


Figure 4: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes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

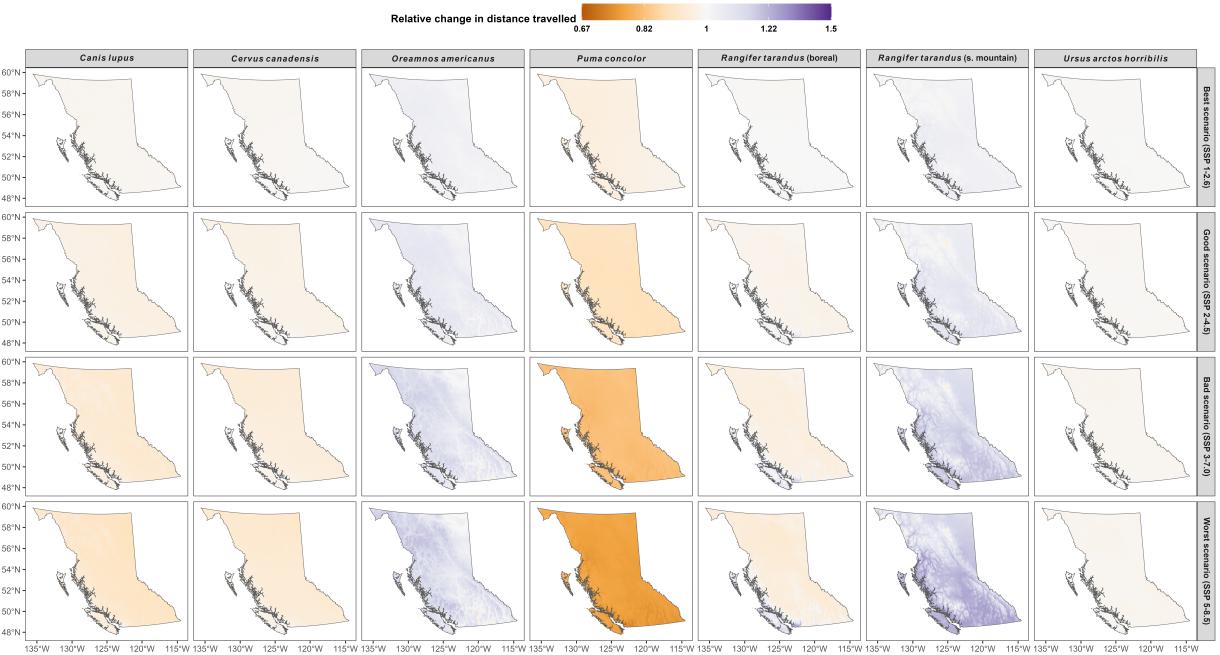


Figure 5: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, 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 0.67 and 1.5 ($\approx 2^{\pm 0.585}$; original data ranged 0.72 to 1.29). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest cover.

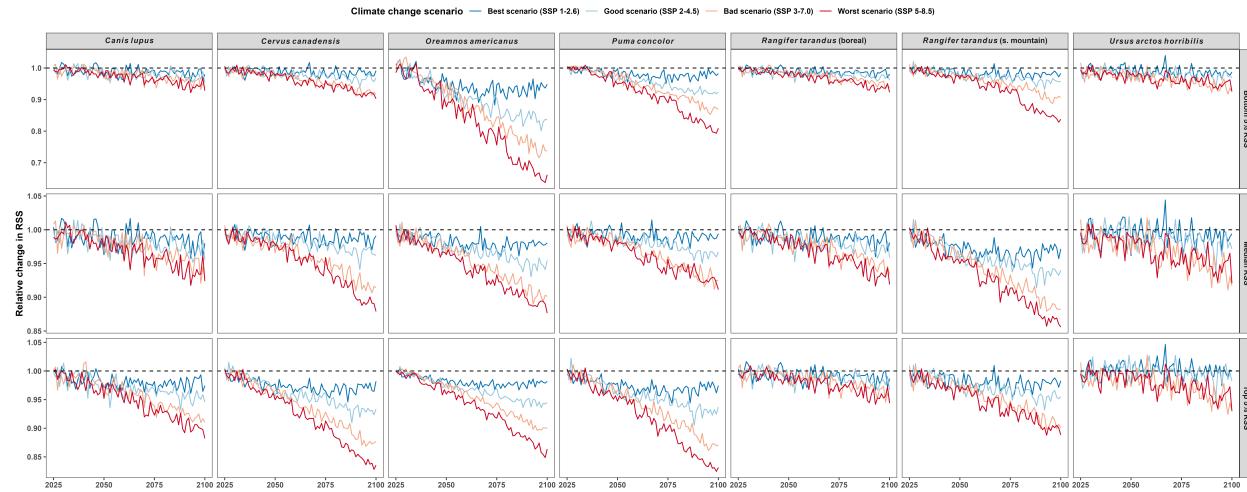


Figure 6: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in RSS for the bottom 5%, median, and top 5% RSS values within the species' current extent. Changes are relative to the mean RSS for each quantile in 2025 across the four Shared Socioeconomic Pathways (SSPs).

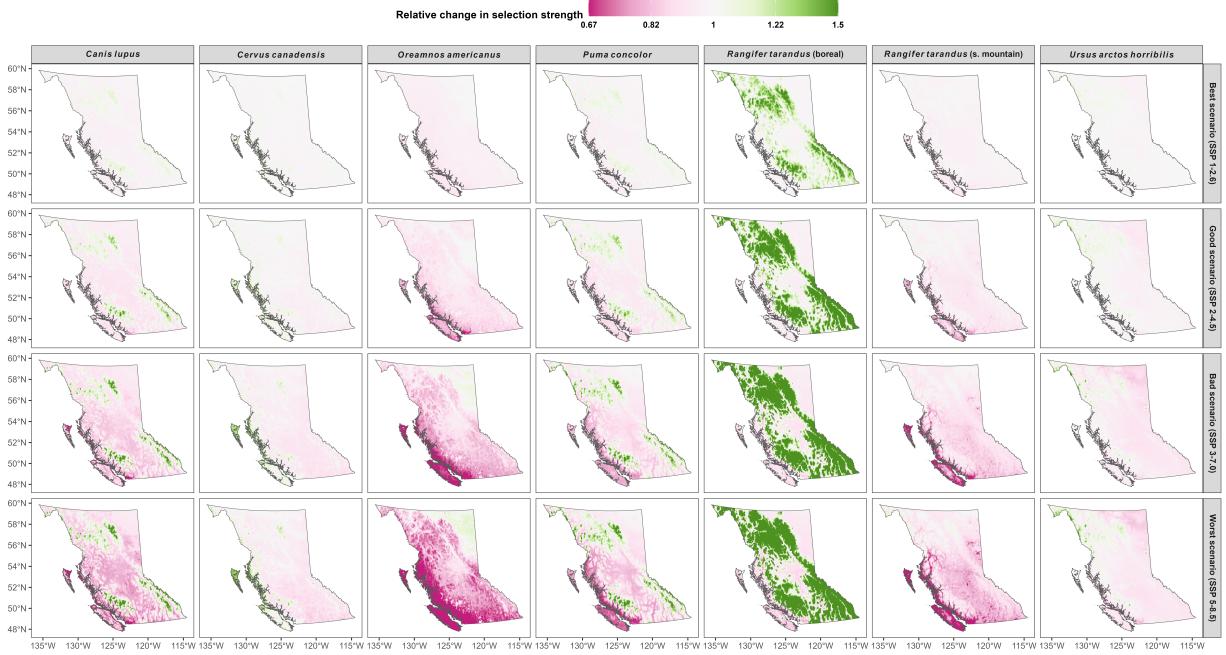


Figure 7: Climate change will impact each species’ habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location’s average RSS in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to 0.67 and 1.5 ($\approx 2^{\pm 0.585}$; original data ranged 0.26 to 117). The increase in boreal caribou’s RSS for high elevations at warmer temperatures was highly uncertain and often not credible at the 95% level.

290 4 Discussion

291 We have demonstrated that temperature is an important determinant of whether, how, and
 292 where mammals move, even while accounting for seasonality (e.g., changes in photoperiod,
 293 hormones, and resources). Disentangling temperature from other drivers is important for
 294 predicting how changes in climate will affect mammalian movement when other drivers re-
 295 main approximately constant. However, predicting mammals’ responses to climate change
 296 becomes increasingly complex as habitats warm and animals are exposed to increasingly
 297 frequent conditions that are both extreme and novel. Predicting mammals’ responses at the
 298 data-scarce fringes of the surface plots in Figs. 2 and 3 comes with substantial uncertainty,
 299 particularly given that the responses are nonlinear. At unusually warm temperatures, mam-
 300 mals (and other homeotherms) overheat [17,26], so their movement behaviour and that of
 301 their competitors, predators, and/or prey can often be substantially different from the be-
 302 haviour at typical temperatures. As extreme temperature events become more frequent and

303 prolonged [38,83], mammals will be increasingly forced towards atypical behaviours that
304 may alter community structures and behaviours, both during such events and afterwards
305 [55]. For instance, changes in climate and phenology impact the life history and behaviour
306 of many hibernating mammals [84], and hot weather can also affects mammals' sleep quality
307 [85] and likelihood to enter torpor [86]. Such changes may alter the frequency and intensity
308 of human-wildlife conflict, especially with the addition of growing pressures from human de-
309 velopment and presence [30,43,87]. At the same time, warmer winters may reduce mammals'
310 energetic expenditure [32,88], increase ease of movement as snow cover and depth decrease
311 [14,15], increase their chances of finding food or being predated upon [89–93], and affect
312 the timing and duration of migrations [14,37,44]. These changes will likely have complex
313 consequences for population and ecosystem structures and dynamics as prey, predators, and
314 competitors experience altered seasonal cycles and increasingly common climate "weirding"
315 [42].

316 Our ability to respond to current and future changes in climate is contingent on our
317 ability to prepare for and predict change. However, predicting animal behaviour becomes
318 increasingly complicated as the conditions animals are exposed to deviate from current, typ-
319 ical conditions, especially when responses are nonlinear and data are sparse. Consequently,
320 we do not present our results as a definitive guide to how mammals in BC will respond
321 to climate change. Instead, we hope they serve as a starting point to (1) demonstrate that
322 mammals' movement rates and habitat selection depend on temperature and (2) how one can
323 estimate mammals' changes in movement behaviour due to climate change. Additionally,
324 communicating uncertainty in one's estimates is crucial in assessing risk probabilistically [94–
325 96]. Recent events in global politics, including global conflicts [97,98] and the rapid rise in
326 generative machine learning [more commonly "AI," see 99,100,101] and its prohibitive energy
327 and water demands [102] and carbon footprint [103], have placed doubt on the feasibility of
328 reaching climate change goals that seemed achievable in the past decade [104]. Mitigating
329 climate change and its consequences will require extensive and widespread collaborative ef-

330 fort [105]. Similarly, protecting a third of the world’s ecosystems [Section H, Targets 2 and 3
331 of 56] appears less tangible as global political and environmental conditions change rapidly
332 and unpredictably [43,106–108]. Achieving the “30 by 30” goal will require active partnership
333 with local Peoples, especially Indigenous Peoples [109,110]. Understanding the consequences
334 of climate change on mammals’ movement behaviour and spatial distribution is a first step
335 towards anticipating and proactively responding to future changes in human-induced rapid
336 environmental change [43,49]. In the following sections, we discuss the implications of our
337 results in more detail. We then expand on consequences for conservation during the 21st
338 century and considerations for future studies.

339 4.1 Effects of temperature on movement rates

340 The lack of common effects of temperature across all species’ movement rates indicates that
341 preparing for future changes will require a variety of physiological and behavioral adaptations
342 as ecological communities respond in complex and interconnected ways. Although our models
343 do not account for explicit physiological or phenological changes, the tensor product terms in
344 Fig. 2 suggest that warmer temperatures cause many species to alter their daily and seasonal
345 activity patterns (most visible in pumas and grizzly bears). For example, when temperatures
346 were above 0°C, pumas moved most at night, but when temperatures were below 0°C they
347 tended to move more throughout the day. Throughout the year, they adapted their tolerance
348 to temperature and moved less when it was relatively hot (for a given time of year), especially
349 in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk,
350 pumas, and boreal caribou when summer temperatures were above 20°C suggests that the
351 increasingly common and intense heat waves across British Columbia will have community-
352 wide impacts on movement rates, encounter rates, and potentially community structure [29].
353 More work is necessary on quantifying interspecific responses to temperature, including the
354 effects of temperature on predation rates [but see: 111,112,113]. The increase in intensity
355 and frequency of extreme heat events [42,83] will likely also impact the occurrence and timing

356 of hibernation [84] and migration or seasonal range expansions [114–116]. However, not all
357 species may be able to adapt at the current rate of climate change [16,49], especially since
358 landscape changes will likely depend not only on the direct effect of temperature but also on
359 cascading changes in the availability and unpredictability of resources [28,117,118].

360 **4.2 Effects of temperature on habitat selection**

361 As with the effects of temperature on movement rates, the lack of common effects of
362 temperature across all species indicates that efficient and proactive habitat conservation
363 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit
364 physiological responses to temperature that may impact movement, such as changes in the
365 phenology of plants, ice, or mammalian physiology or behaviour (e.g., moulting, migration),
366 other than as direct responses to temperature. Consequently, the behavioural changes we
367 present should be interpreted carefully. While some seasonal cycles do not depend directly
368 on temperature and may thus not be impacted directly by climate change [such as those
369 driven by photoperiod, see 119], the predictions we present also rely on the assumption
370 that mammals will not adapt these seasonal cycles to temperature-dependent cues, such
371 as weather [120] or forage availability [121], which may not be correct. Additionally, it is
372 important to stress the distinction between habitat selection and quality. While animals tend
373 to select for high-quality habitats [3,122], high selection strength can also be a consequence
374 of an ecological trap [123,124].

375 **4.3 Predicted changes in movement during the 21st century**

376 Achieving the goals laid out by the “30 by 30” conservation initiative [Section H, Tar-
377 gets 2 and 3 of 56] will require careful planning but often also rapid action. In the case
378 of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the end
379 of 2023 [125,126]. Additionally, efficient and effective conservation will require collabora-
380 tion with Indigenous and local communities to ensure Treaties are respected in the process

[52,109,110,e.g., 127] while also actively preparing for future change [128,129]. The large range in predicted changes by 2100 (both across species and within species' current ranges) and high spatial heterogeneity in Fig. 7 highlight the need for careful planning that incorporates not only reliable estimates of change but also pragmatic and communicable measures of uncertainty and variability around such estimates. The width of the prediction intervals in Fig. 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 and prey availability [28], encounter rates [29,89], population dynamics [130], competitive pressure [131], and predation risk [132]. This complexity results in the great variation among the responses of different species (and individuals), especially as populations a rapid cascade of change [47] and animals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces [30,43,44,133–135]. As selection strength for current ranges changes (and likely decreases), some animals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased extinction risk [136].

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 [71,137,138], (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 behaviour becomes highly complex when responses are non-linear, especially when changes depend on many interacting factors [35] and one is interested in predicting responses in extreme conditions for which data are scarce [139]. We address each consideration in the following three paragraphs.

407 While the `ctmm` models produced scale-independent estimates of speed [i.e., model inter-
408 pretation is independent of sampling interval: 71], the accuracy, size, and stability of speed
409 estimates still depended on the GPS sampling frequency. This is because coarsely-sampled
410 movement data contains information on large-scale movements (e.g., range crossings, mi-
411 grations) but not fine-scale movements [e.g., first-order habitat selection *sensu* 80, also see
412 137]. Using the boreal caribou as an example, the 13-hour sampling interval allows us to
413 reasonably estimate the caribou's movement path at a temporal scale of approximately 13
414 hours (or greater), but we cannot produce reasonable movement trajectories at a much finer
415 (e.g., hourly) scale. Consequently, we suggest being cautious when comparing estimated
416 movement behaviours across species, even though all predictions have been corrected to the
417 hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Thus, sampling
418 schedules should be fine enough to reconstruct animals' movement at a sufficiently fine scale.
419 Good estimates of an animal's speed and its movement path require telemetry locations to
420 be taken more often than the animal's directional persistence [71], so that, on average, the
421 dataset contains multiple locations in between changes in direction. What constitutes a
422 change in direction depends on what movement scale one is investigating. Small-scale move-
423 ments and first-order spatial selection will require more frequent sampling than migratory
424 movement or second- and third-order spatial selection. While `ctmm` movement models are
425 scale-invariant in that any model can be scaled to larger or smaller areas and timescales, the
426 model estimates are not independent of the scale of the sampling frequency.

427 When landscapes are relatively predictable across years, a larger number of sampled in-
428 dividuals is likely preferable over longer, multi-year telemetries. This allows one to quantify
429 the variance across individuals, including the range of conditions and environments that indi-
430 vidual animals are in. A good estimate of inter-individual variance provides better coefficient
431 estimates along with more appropriate measures of uncertainty. However, when conditions
432 across years are relatively stochastic, multi-year telemetries allow one to better estimate
433 inter-annual variation without conflating it with inter-individual differences. In either case,

⁴³⁴ carefully-designed sampling schedules and (Bayesian) hierarchical models can provide good
⁴³⁵ estimates of the effects of interested along with appropriate measures of uncertainty [96,140].

⁴³⁶ Quantifying and communicating uncertainty become particularly important as we predict
⁴³⁷ for conditions for which we have little to no data, such as during extreme events. Addition-
⁴³⁸ ally, estimating nonlinear trends is particularly difficult near the edges of the data (e.g.,
⁴³⁹ extremely high temperatures), especially when data is scarce. Consequently, the estimated
⁴⁴⁰ responses at the fringes of the surfaces in figures 2 and 3 are more likely likely to be poorly
⁴⁴¹ estimated, particularly in the case of HRSFs, but increasing data density throughout the
⁴⁴² resource-temperature surfaces can ameliorate the issue. Preparing for future changes re-
⁴⁴³ quires some degree of inevitable risk, so it is imperative that models be statistically sound
⁴⁴⁴ and interpretable, and that results are communicated transparently and clearly to decision
⁴⁴⁵ makers and the public alike.

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