

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

Stefano Mezzini<sup>1,2</sup>      Chris H. Fleming<sup>3,4</sup>      Siobhan Darlington<sup>1,2</sup>

Adam T. Ford<sup>1,2</sup>      Karen E. Hodges<sup>1,2</sup>      Kirk Safford<sup>5</sup>

Robert Serrouya<sup>1,2,6</sup>      Michael J. Noonan<sup>1,2,7</sup>

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

<sup>2</sup> Department of Biology, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

<sup>3</sup> Department of Biology, University of Central Florida, Orlando, Florida 32816, United States.

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

<sup>5</sup> BC Parks

<sup>6</sup> Wildlife Science Centre, Biodiversity Pathways, University of British Columbia Okanagan, Revelstoke, British Columbia, Canada.

<sup>7</sup> Department of Computer Science, Math, Physics, and Statistics, The University of British Columbia Okanagan, Kelowna, British Columbia, Canada.

**Article type:** Research article

**Words in abstract:** 241

**Words in main text:** 6328

**Figures:** 7

**Tables:** 2

**References:** 141 (updated on 2025-05-16)

**Appendices:** 2

**Key words:** climate change, temperature, mammals, animal movement, movement behavior, habitat selection

## Abstract

Recent widespread warming has caused many terrestrial mammals to change when, how, and where they move, with cascading effects on fitness, habitat selection, and community structure. Previous studies have quantified the effects of temperature on mammalian movement behaviour, but few have quantified the effects of future climate change. Consequently, it is still unclear how and where mammals will move in the 21<sup>st</sup> century. We address this gap by using Continuous-Time Movement Models and Hierarchical Generalized Additive Models to quantify the effects of temperature on the probability of moving, the speed when moving, and the habitat selection of six species throughout British Columbia, Canada. We show that temperature is a strong determinant of when, how, and where mammals move, and that climate change will impact mammals' movement rates and habitat selection throughout the 21<sup>st</sup> century. We found no common effects of temperature on the species' movement rates, so we suggest that species' estimated responses be interpreted jointly when making inferences about how climate change will impact ecological communities. In contrast, habitat selection strength decreased for all species within their current ranges, suggesting that all six species will shift their range in the coming decades. As climate change exposes mammals to novel environmental conditions, predicting changes in animal behavior and community structure will become crucial for effective and proactive conservation. We thus conclude by providing suggestions for conservation and future research while calling for a more holistic and collaborative framework.

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

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

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

<sup>21</sup> In the last 200 years, many ecosystems experienced widespread warming that resulted  
<sup>22</sup> in milder and shorter winters, hotter and longer summers, and a greater risk of extremely  
<sup>23</sup> high temperatures and severe forest fires [38,39]. Over the next 100 years, these changes  
<sup>24</sup> are expected to worsen and continue to impact mammals’ fitness, movement behaviour,  
<sup>25</sup> and habitat selection as animals cope with growing heat stress [40,41] and more frequent  
<sup>26</sup> 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 21<sup>st</sup> 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 (wolves: *Canis lupus*, elk:  
52 *Cervus canadensis*, mountain goats: *Oreamnos americanus*, pumas: *Puma concolor*, boreal  
53 and southern mountain caribou: *Rangifer tarandus*, and grizzly bears: *Ursus arctos horribilis*;

54 Table 1). Using over 25 years of telemetry data throughout a large spatial range of British  
 55 Columbia and hourly air temperature data, we estimate how mammals altered their proba-  
 56 bility of movement, speed when moving, and habitat selection in response to temperature.  
 57 We then pair the estimated responses with climate change projections to forecast the species'  
 58 movement during the 21<sup>st</sup> century under different climate-change scenarios [referred to as  
 59 Shared Socioeconomic Pathways, SSPs – see 57]. We disentangle the direct and indirect  
 60 effects of temperature on the movement behaviour of terrestrial mammals and discuss the  
 61 consequences of these changes at the individual, population, and landscape levels.

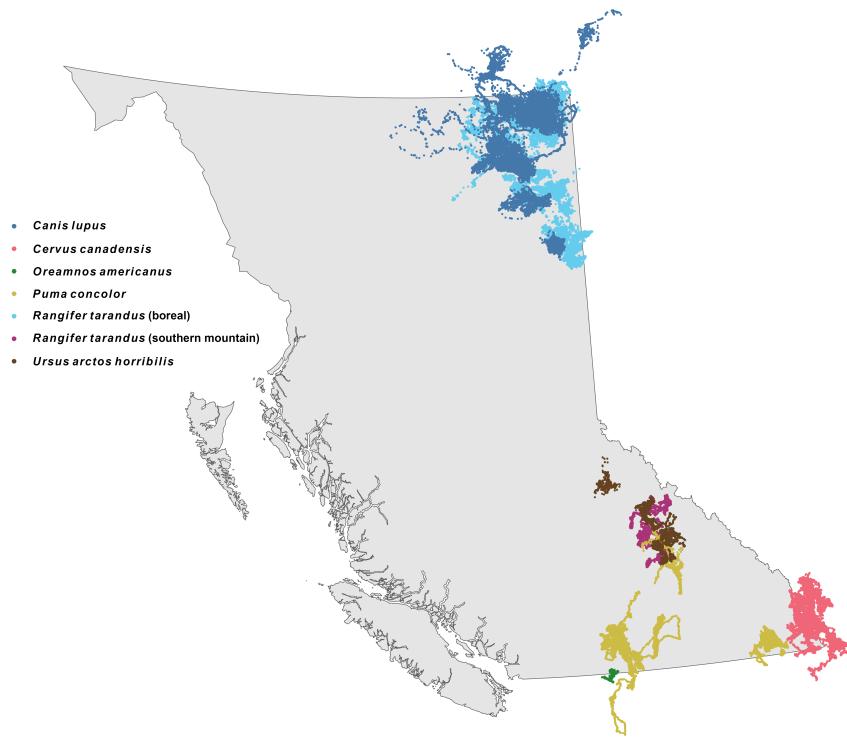


Figure 1: GPS telemetry data for the six species in this study.

Table 1: Start and end of the GPS telemetries along with the median sampling interval ( $\Delta t$ ; stratified by individual), number of animals (Animals), and number of animals with resolved speed (Has speed) for each of the species in this study.

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

Species	Start	End	$\Delta t$ (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](http://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  $0.08^\circ$  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  $\chi^2$ -distributed. The function we used is available 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-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. B3).

### 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 fits of the two sets of models. We provide the relevant Directed Acyclical Graphs in the Appendix (Figs. B1-B2).

#### 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. B1-B2).

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. B13), especially after

211 accounting for weighting based on the degree of autocorrelation and the number of home  
212 range crossings (Fig. B14).

### 213 3 Results

214 Data were relatively scarce for temperatures lower than  $-20^{\circ}\text{C}$  or above  $20^{\circ}\text{C}$  (Fig. B4).  
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

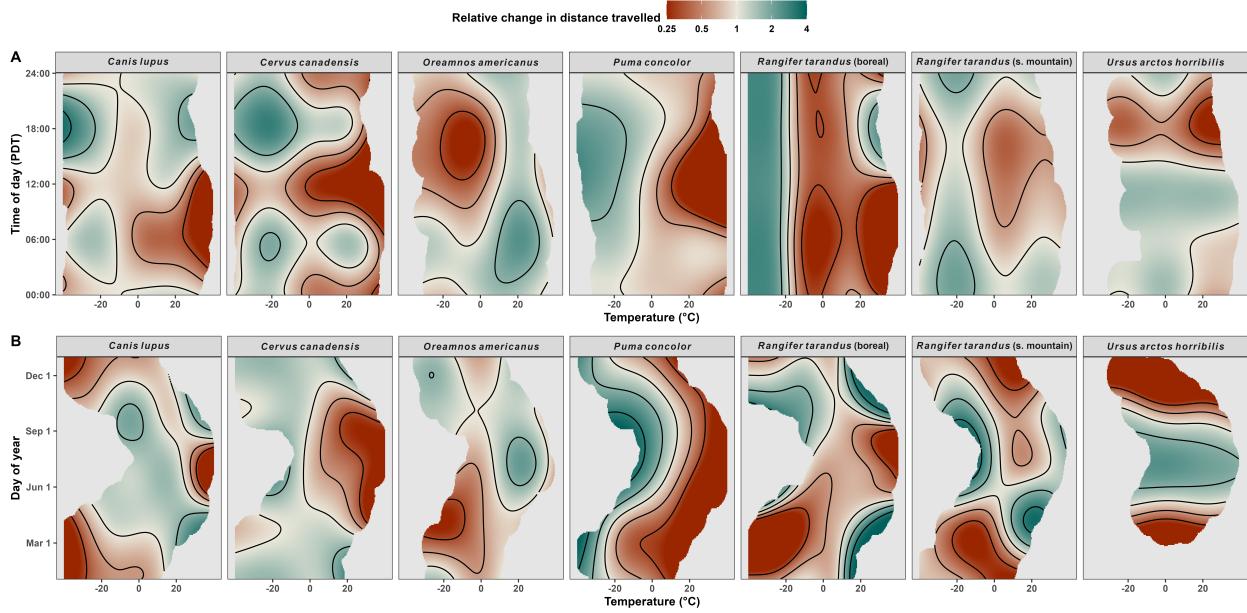
222 Near  $0^{\circ}\text{C}$ , wolves preferred dense forest cover ( $\gtrapprox 50\%$ ) high elevations, and distances  
223 from water  $< 10 \text{ km}$ ; elk preferred intermediate forest cover, elevations between 1 and 2 km,  
224 and distances from water of 5–15 km; mountain goats preferred sparse ( $< 50\%$ ) 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

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

231 There was relatively strong agreement between models with and without temperature  
232 (Figs. B5 and S13), but including temperature always resulted in better fits. All analyses  
233 of deviance showed that temperature significantly affected movement behavior (all p-values  
234  $< 2.2 \times 10^{-16}$ ; all  $\Delta AIC \geq 342$ ; see Table B1 and the analyses of deviance in Appendix B).  
235 The only exception to this was the mountain goat HRSF, where the addition of tempera-  
236 ture resulted in a simpler model (lower model degrees of freedom) that fit the data better  
237 (lower deviance), and hence no test was necessary to show that the inclusion of temperature  
238 produced a better fit.

### 239 **3.1 Effects of temperature on movement rates**

240 The effects of temperature on movement rates varied in both direction and magnitude across  
241 species, even after accounting for differences in daily and seasonal activity (e.g., sleeping,  
242 migration, hibernation; see Figs. B6-B8). Smooth interaction terms were well-behaved and  
243 indicated clear shifts in activity over time of day and day of year for all species. The models  
244 explained reasonably high proportions of the deviance (10.7% for the binomial model and  
245 79.3% for the Gamma model) and had good in-sample prediction (Fig. B9). All species  
246 adapted their daily and seasonal movement behaviour to changes in temperature (Fig. 2).  
247 For example, wolves, elk, pumas, and boreal caribou reduced their mid-day and summer  
248 movement rates when temperatures were above 20°C. However, uncertainties around the  
249 estimated effects were often higher at extreme temperatures due to data scarcity. All species'  
250 estimated probability of moving decreased with sampling intervals approximately above 1  
251 hour, and most species' estimated speed when moving decreased monotonically with sampling  
252 interval, although the estimated trends were highly uncertain for some species (Fig. B10).



**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 1<sup>st</sup> (A) and day of year at 12:00 PDT (B). Predictions in the surface plots extend to 10% of the range away from each datum. The color bar is on the log<sub>2</sub> scale to help visualize patterns in doubling, and values are capped to  $2^{\pm 2}$  for ease of readability.

### 253 3.2 Effects of temperature on habitat selection

254 Species' relative selection strength (RSS) was generally strongest for elevation and weak-

255 est for forest cover, but species' RSS for resources depended on temperature. Changes in

256 RSS with temperature were also strongest for elevation and generally weakest distance from

257 water, but there were no common trends across all species for any of the three resources.

258 All species, with the exception of pumas, exhibited a clear temperature-dependent shift

259 in their preference for forest cover. At higher temperatures, wolves, mountain goats, and

260 grizzly bears became less selective for forest cover, while elk and caribou shifted towards

261 more intermediate forest cover without much of a change in preference width. All species

262 shifted elevationally with temperature, although boreal caribou did not exhibit as strong

263 of a change. As temperatures rose, elk, mountain goats, and pumas increased in elevation,

264 while boreal wolves, southern mountain caribou, and grizzly bears decreased in elevation.

265 Most species generally remained within 5 km of water, and temperature did not affect their

266 selection strength as much as for the other two resources. Again, estimated RSS values were

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

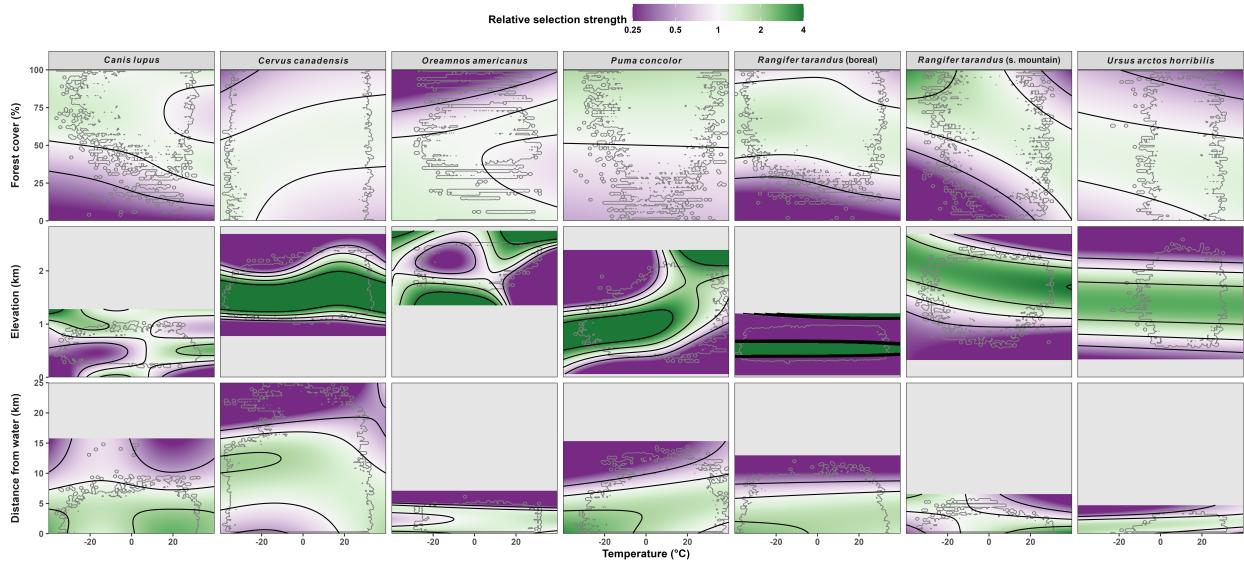


Figure 3: **Temeperature strongly affects mammals' habitat selection.** Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were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

### 268 3.3 Predicted changes in movement during the 21<sup>st</sup> century

269 Species varied in both the direction and magnitude of predicted change in distance traveled,  
 270 but worse climate-change scenarios always corresponded to greater absolute changes in be-  
 271 haviour (Figs. 4, S11, and S12). Under the best-case scenario, absolute changes by 2100  
 272 were small (approximately 0% to 4%), while under the worst-case scenario absolute changes  
 273 ranged from  $\sim 2\%$  (grizzly bear) to  $\sim 25\%$  (pumas), although the models did not explicitly  
 274 account for changes in hibernation phenology. Throughout BC (Fig. 5), all species showed  
 275 little to no absolute change under the best-case scenario (approximately 0-4% relative to  
 276 2025, on average), and approximately 2-25% average absolute change under the worst-case  
 277 scenario, but the predicted changes varied spatially due to heterogeneity in climate change.  
 278 Again, absolute changes were smallest under the best-case scenario and greatest under the  
 279 worst-case scenario for all species.

280 All species exhibited a decrease in RSS within their current range, irrespective of climate  
 281 change scenario. Changes were often were only between -1% and -3% under the best-case  
 282 scenario but they ranged from -8% to -14% under the worst-case scenario (6). As with

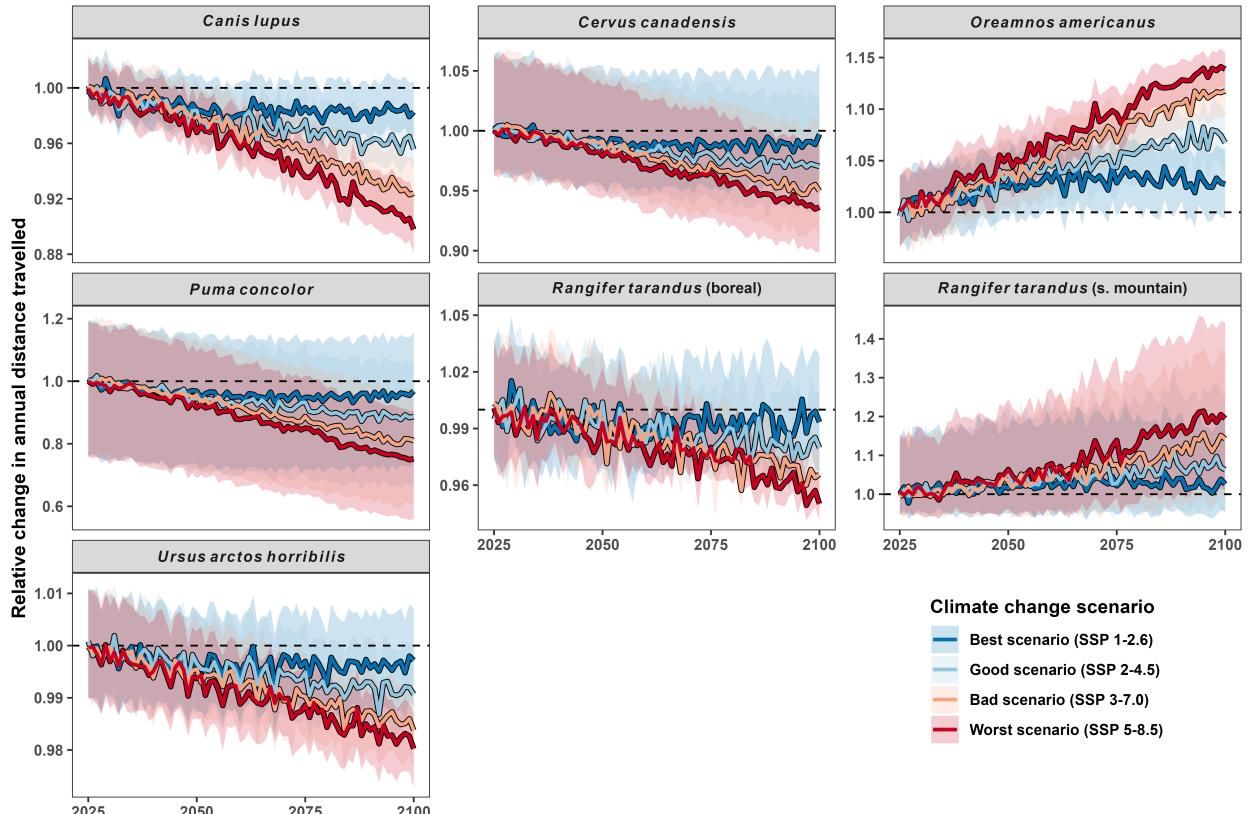
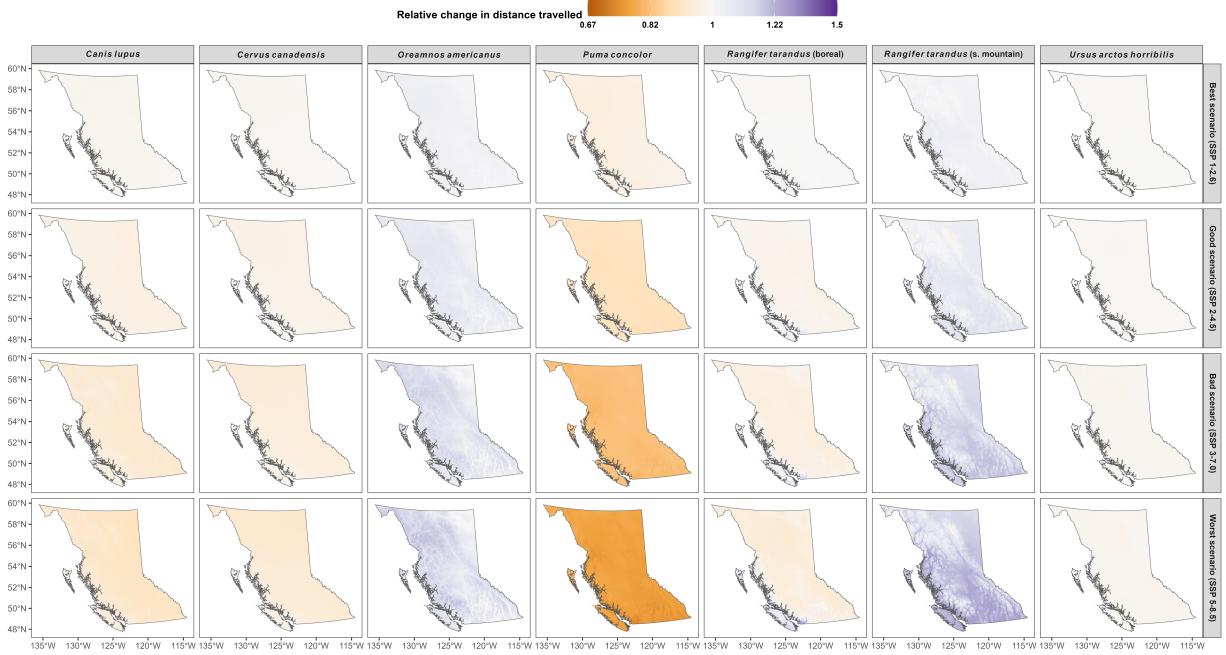


Figure 4: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes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

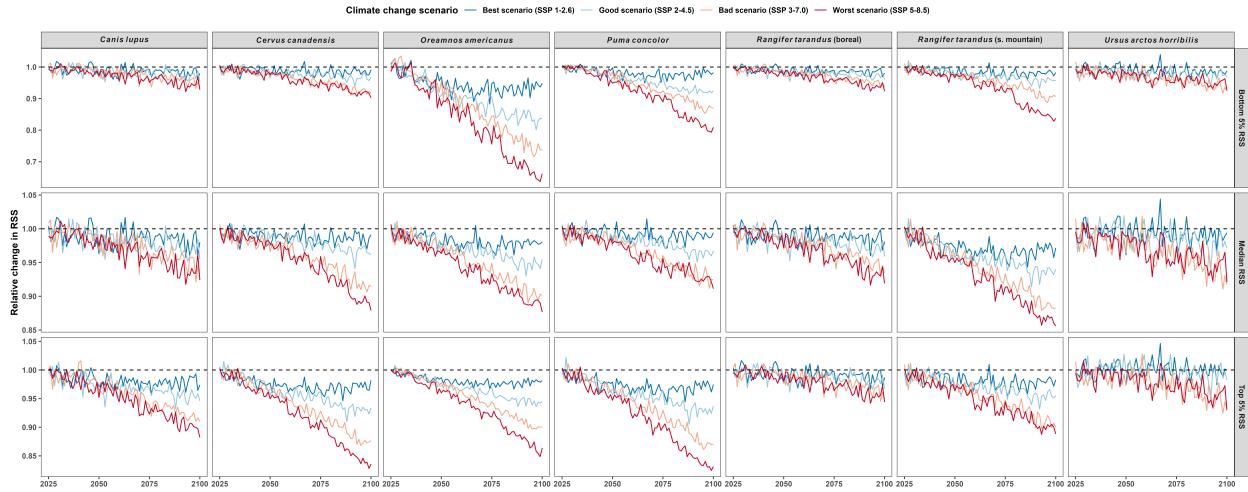


**Figure 5: Climate change will impact each species' movement rates differently.** The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values  $< 1$  indicate a decrease, 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.

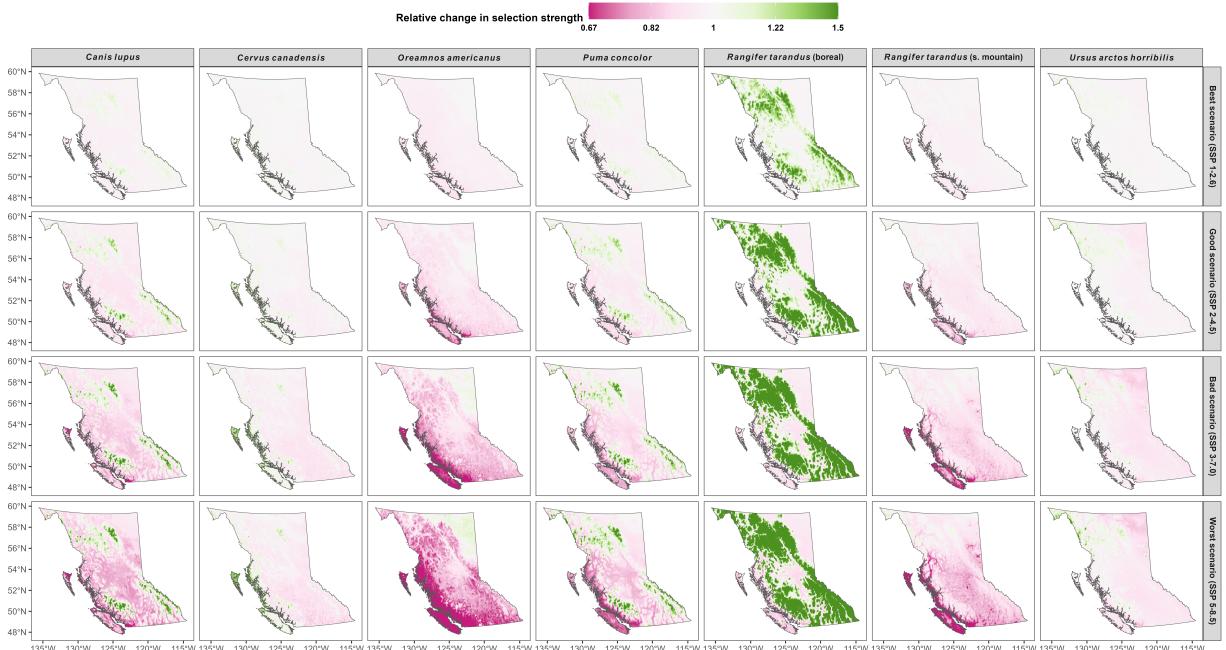
283 distance traveled, the change in RSS in 2100 varied throughout BC for all species (Fig. 7).  
 284 All species were predicted to exhibit a decrease in RSS throughout most of BC, with the  
 285 exception of boreal caribou, which had a predicted increase in approximately 67% of the  
 286 province, including their current range. The increase was in great part due to the estimated  
 287 increase in selection for high-elevation areas that are well outside the population's current  
 288 range.

## 289 4 Discussion

290 We have demonstrated that temperature is an important determinant of whether, how, and  
 291 where mammals move, even while accounting for seasonality (e.g., changes in photoperiod,  
 292 hormones, and resources). Disentangling temperature from other drivers is important for  
 293 predicting how changes in climate will affect mammalian movement when other drivers re-  
 294 main approximately constant. However, predicting mammals' responses to climate change



**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 ( $\approx 2^{0.585}$ ; 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.

becomes increasingly complex as habitats warm and animals are exposed to increasingly frequent conditions that are both extreme and novel. Predicting mammals' responses at the data-scarce fringes of the surface plots in Figs. 2 and 3 comes with substantial uncertainty, particularly given that the responses are nonlinear. At unusually warm temperatures, mammals (and other homeotherms) overheat [17,26], so their movement behaviour and that of their competitors, predators, and/or prey can often be substantially different from the behaviour at typical temperatures. As extreme temperature events become more frequent and prolonged [38,82], mammals will be increasingly forced towards atypical behaviours that may alter community structures and behaviours, both during such events and afterwards [55,83,84]. For instance, changes in climate and phenology impact the life history and behaviour of many hibernating mammals [85], and hot weather can also affects mammals' sleep quality [86] and likelihood to enter torpor [87]. Such changes may alter the frequency and intensity of human-wildlife conflict, especially with the addition of growing pressures from human development and presence [30,43,88]. At the same time, warmer winters may reduce mammals' energetic expenditure [32,89], increase ease of movement as snow cover and depth decrease [14,15], increase their chances of finding food or being predated upon [90–94], and affect the timing and duration of migrations [14,37,44]. These changes will likely have complex consequences for population and ecosystem structures and dynamics as prey, predators, and competitors experience altered seasonal cycles and increasingly common climate “weirding” [42].

Our ability to respond to current and future changes in climate is contingent on our ability to prepare for and predict change. However, predicting animal behaviour becomes increasingly complicated as the conditions animals are exposed to deviate from current, typical conditions, especially when responses are nonlinear and data are sparse. 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 behaviour due to climate change. Additionally, communicating uncertainty in one's estimates is crucial in assessing risk probabilistically [95–97]. Recent events in global politics, including global conflicts [98,99] and the rapid rise in generative machine learning [more commonly: “AI,” see 100,101,102] and its prohibitive energy and water demands [103] and carbon footprint [104], have placed doubt on the feasibility of reaching climate change goals that seemed achievable in the past decade [105]. Mitigating climate change and its consequences will require extensive and widespread collaborative effort [106]. Similarly, protecting a third of the world’s ecosystems [Section H, Targets 2 and 3 of 56] appears less tangible as global political and environmental conditions change rapidly and unpredictably [43,107–109]. Achieving the “30 by 30” goal will require active partnership with local Peoples, especially Indigenous Peoples [110,111]. Understanding the consequences of climate change on mammals’ movement behaviour and spatial distribution is a first step towards anticipating and proactively responding to future changes in human-induced rapid environmental change [43,49]. In the following sections, we discuss the implications of our results in more detail. We then expand on consequences for conservation during the 21<sup>st</sup> century and considerations for future studies.

#### 4.1 Effects of temperature on movement rates

The lack of common effects of temperature across all species’ movement rates indicates that preparing for future changes will require a variety of physiological and behavioral adaptations as ecological communities respond in complex and interconnected ways. Although our models do not account for explicit physiological or phenological changes, the tensor product terms in Fig. 2 suggest that warmer temperatures cause many species to alter their daily and seasonal activity patterns (most visible in pumas and grizzly bears). For example, when temperatures were above 0°C, pumas moved most at night, but when temperatures were below 0°C they tended to move more throughout the day. Throughout the year, they adapted their tolerance to temperature and moved less when it was relatively hot (for a given time of year), especially

348 in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk,  
349 pumas, and boreal caribou when summer temperatures were above 20°C suggests that the  
350 increasingly common and intense heat waves across British Columbia will have community-  
351 wide impacts on movement rates, encounter rates, and potentially community structure [29].  
352 More work is necessary on quantifying interspecific responses to temperature, including the  
353 effects of temperature on predation rates [but see: 112,113,114]. The increase in intensity  
354 and frequency of extreme heat events [42,82] will likely also impact the occurrence and timing  
355 of hibernation [85] and migration or seasonal range expansions [115–117]. However, not all  
356 species may be able to adapt at the current rate of climate change [16,49], especially since  
357 landscape changes will likely depend not only on the direct effect of temperature but also on  
358 cascading changes in the availability and unpredictability of resources [28,118,119].

## 359 **4.2 Effects of temperature on habitat selection**

360 As with the effects of temperature on movement rates, the lack of common effects of  
361 temperature across all species indicates that efficient and proactive habitat conservation  
362 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit  
363 physiological responses to temperature that may impact movement, such as changes in the  
364 phenology of plants, ice, or mammalian physiology or behaviour (e.g., moulting, migration),  
365 other than as direct responses to temperature. Consequently, the behavioural changes we  
366 present should be interpreted carefully. While some seasonal cycles do not depend directly  
367 on temperature and may thus not be impacted directly by climate change [such as those  
368 driven by photoperiod, see 120], the predictions we present also rely on the assumption  
369 that mammals will not adapt these seasonal cycles to temperature-dependent cues, such  
370 as weather [121] or forage availability [122], which may not be correct. Additionally, it is  
371 important to stress the distinction between habitat selection and quality. While animals tend  
372 to select for high-quality habitats [3,123], high selection strength can also be a consequence  
373 of an ecological trap [124,125].

<sup>374</sup> **4.3 Predicted changes in movement during the 21<sup>st</sup> century**

<sup>375</sup> Achieving the goals laid out by the “30 by 30” conservation initiative [Section H, Tar-  
<sup>376</sup> gets 2 and 3 of 56] will require careful planning but often also rapid action. In the case  
<sup>377</sup> of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the end  
<sup>378</sup> of 2023 [126,127]. Additionally, efficient and effective conservation will require collabora-  
<sup>379</sup> tion with Indigenous and local communities to ensure Treaties are respected in the process  
<sup>380</sup> [52,110,111,e.g., 128] while also actively preparing for future change [129,130]. The large  
<sup>381</sup> range in predicted changes by 2100 (both across species and within species’ current ranges)  
<sup>382</sup> and high spatial heterogeneity in Fig. 7 highlight the need for careful planning that incorpo-  
<sup>383</sup> rates not only reliable estimates of change but also pragmatic and communicable measures  
<sup>384</sup> of uncertainty and variability around such estimates. The width of the prediction intervals  
<sup>385</sup> in Fig. 4 suggest that spatial and intra-individual variation should be accounted for when  
<sup>386</sup> deciding the location and size of protected areas. Accurate estimates of the effects of changes  
<sup>387</sup> in temperature on mammals’ movement require a holistic view of the direct effects of tem-  
<sup>388</sup> perature on mammals’ movement directly as well as its effects on other drivers of movement,  
<sup>389</sup> such as forage and prey availability [28], encounter rates [29,90], population dynamics [131],  
<sup>390</sup> competitive pressure [132], and predation risk [133]. This complexity results in the great vari-  
<sup>391</sup> ation among the responses of different species (and individuals), especially as populations  
<sup>392</sup> a rapid cascade of change [47] and animals face increasing pressures from human activity,  
<sup>393</sup> including habitat fragmentation, habitat loss, and greater human presence in wild spaces  
<sup>394</sup> [30,43,44,134–136]. As selection strength for current ranges changes (and likely decreases),  
<sup>395</sup> some animals may disperse, relocate to a new habitat, or remain within the current range  
<sup>396</sup> despite the reduced fitness and increased extinction risk [83,84,137].

<sup>397</sup> **4.4 Considerations for future studies**

<sup>398</sup> Our work highlights three central considerations for future research: (1) telemetry sam-  
<sup>399</sup> pling rates should be designed primarily in relation to the movement timescales of the species

400 of interest [71,138,139], (2) the number of individuals tracked and the length of each telem-  
401 try should depend not just on population size but also environmental stability, and (3)  
402 predicting changes in movement behaviour becomes highly complex when responses are non-  
403 linear, especially when changes depend on many interacting factors [35] and one is interested  
404 in predicting responses in extreme conditions for which data are scarce [140]. We address  
405 each consideration in the following three paragraphs.

406 While the `ctmm` models produced scale-independent estimates of speed [i.e., model inter-  
407 pretation is independent of sampling interval: 71], the accuracy, size, and stability of speed  
408 estimates still depended on the GPS sampling frequency. This is because coarsely-sampled  
409 movement data contains information on large-scale movements (e.g., range crossings, mi-  
410 grations) but not fine-scale movements [e.g., first-order habitat selection *sensu* 80,also see  
411 138]. Using the boreal caribou as an example, the 13-hour sampling interval allows us to  
412 reasonably estimate the caribou's movement path at a temporal scale of approximately 13  
413 hours (or greater), but we cannot produce reasonable movement trajectories at a much finer  
414 (e.g., hourly) scale. Consequently, we suggest being cautious when comparing estimated  
415 movement behaviours across species, even though all predictions have been corrected to the  
416 hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Thus, sampling  
417 schedules should be fine enough to reconstruct animals' movement at a sufficiently fine scale.  
418 Good estimates of an animal's speed and its movement path require telemetry locations to  
419 be taken more often than the animal's directional persistence [71], so that, on average, the  
420 dataset contains multiple locations in between changes in direction. What constitutes a  
421 change in direction depends on what movement scale one is investigating. Small-scale move-  
422 ments and first-order spatial selection will require more frequent sampling than migratory  
423 movement or second- and third-order spatial selection. While `ctmm` movement models are  
424 scale-invariant in that any model can be scaled to larger or smaller areas and timescales, the  
425 model estimates are not independent of the scale of the sampling frequency.

426 When landscapes are relatively predictable across years, a larger number of sampled in-

427 individuals is likely preferable over longer, multi-year telemetries. This allows one to quantify  
428 the variance across individuals, including the range of conditions and environments that indi-  
429 vidual animals are in. A good estimate of inter-individual variance provides better coefficient  
430 estimates along with more appropriate measures of uncertainty. However, when conditions  
431 across years are relatively stochastic, multi-year telemetries allow one to better estimate  
432 inter-annual variation without conflating it with inter-individual differences. In either case,  
433 carefully-designed sampling schedules and (Bayesian) hierarchical models can provide good  
434 estimates of the effects of interested along with appropriate measures of uncertainty [97,141].

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

445 **References**

- 446 1. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement  
447 ecology paradigm for unifying organismal movement research. *Proceedings of the National  
448 Academy of Sciences* [Internet]. 2008 [cited 2022 Mar 9];105:19052–9. Available from:  
449 <https://pnas.org/doi/full/10.1073/pnas.0800375105>
- 450 2. Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical Population  
451 Biology* [Internet]. 1976 [cited 2024 Jan 31];9:129–36. Available from: [https://linkinghub.elsevier.com/retrieve/pii/004058097690040X](https://linkinghub.<br/>452 elsevier.com/retrieve/pii/004058097690040X)
- 453 3. Kacelnik A, Krebs JR, Bernstein C. The ideal free distribution and predator-prey popula-  
454 tions. *Trends in Ecology & Evolution* [Internet]. 1992 [cited 2024 Jan 31];7:50–5. Available  
455 from: <https://linkinghub.elsevier.com/retrieve/pii/016953479290106L>
- 456 4. Winter VA, Smith BJ, Berger DJ, Hart RB, Huang J, Manlove K, et al. Forecasting animal  
457 distribution through individual habitat selection: Insights for population inference and  
458 transferable predictions. *Ecography* [Internet]. 2024 [cited 2024 Oct 9];e07225. Available  
459 from: <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.07225>
- 460 5. Peterson AN, Soto AP, McHenry MJ. Pursuit and Evasion Strategies in the Predator–  
461 Prey Interactions of Fishes. *Integrative and Comparative Biology* [Internet]. 2021 [cited  
462 2025 Jan 15];61:668–80. Available from: [https://academic.oup.com/icb/article/61/2/668/6290712](https://academic.oup.com/icb/article/61/2/668/<br/>463 6290712)
- 464 6. Bartashevich P, Herbert-Read JE, Hansen MJ, Dhellemmes F, Domenici P, Krause J,  
465 et al. Collective anti-predator escape manoeuvres through optimal attack and avoidance  
466 strategies. *Communications Biology* [Internet]. 2024 [cited 2025 Jan 15];7:1586. Available  
467 from: <https://www.nature.com/articles/s42003-024-07267-2>
- 468 7. Tan M, Zhang S, Stevens M, Li D, Tan EJ. Antipredator defences in motion: Animals  
469 reduce predation risks by concealing or misleading motion signals. *Biological Reviews*  
470 [Internet]. 2024 [cited 2025 Jan 15];99:778–96. Available from: [https://onlinelibrary.wiley.com/doi/10.1111/bior.13620](https://onlinelibrary.<br/>471 wiley.com/doi/10.1111/bior.13620)

- 471      [wiley.com/doi/10.1111/brv.13044](https://doi.org/10.1111/brv.13044)
- 472    8. McNab BK. Body Weight and the Energetics of Temperature Regulation. *Journal*  
473    of Experimental Biology [Internet]. 1970 [cited 2025 May 9];53:329–48. Available  
474    from: <https://journals.biologists.com/jeb/article/53/2/329/21468/Body-Weight-and-the-Energetics-of-Temperature>
- 475
- 476    9. Taylor CR, Heglund NC, Maloiy GMO. Energetics and mechanics of terrestrial loco-  
477    motion. I. Metabolic energy consumption as a function of speed and body size in birds  
478    and mammals. *Journal of Experimental Biology* [Internet]. 1982 [cited 2023 Jun 22];97:1–  
479    21. Available from: <https://journals.biologists.com/jeb/article/97/1/1/34642/Energetics-and-mechanics-of-terrestrial-locomotion>
- 480
- 481    10. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory  
482    of ecology. *Ecology* [Internet]. 2004 [cited 2022 Mar 3];85:1771–89. Available from: <http://doi.wiley.com/10.1890/03-9000>
- 483
- 484    11. Fuller A, Mitchell D, Maloney SK, Hetem RS. Towards a mechanistic understanding  
485    of the responses of large terrestrial mammals to heat and aridity associated with climate  
486    change. *Climate Change Responses* [Internet]. 2016 [cited 2025 Jan 16];3:10. Available  
487    from: <http://climatechangeresponses.biomedcentral.com/articles/10.1186/s40665-016-0024-1>
- 488
- 489    12. Jahn M, Seebacher F. Variations in cost of transport and their ecological conse-  
490    quences: A review. *Journal of Experimental Biology* [Internet]. 2022 [cited 2025 Jan  
491    15];225:jeb243646. Available from: <https://journals.biologists.com/jeb/article/225/15/jeb243646/276242/Variations-in-cost-of-transport-and-their>
- 492
- 493    13. Montgomery RA, Redilla KM, Moll RJ, Van Moorter B, Rolandsen CM, Millspaugh JJ,  
494    et al. Movement modeling reveals the complex nature of the response of moose to ambient  
495    temperatures during summer. *Journal of Mammalogy* [Internet]. 2019 [cited 2024 Aug  
496    8];100:169–77. Available from: <https://academic.oup.com/jmammal/article/100/1/169/5299335>
- 497

- 498 14. Leclerc M, Leblond M, Le Corre M, Dussault C, Côté SD. Determinants of migration  
499 trajectory and movement rate in a long-distance terrestrial mammal. Reyna R, editor.  
500 Journal of Mammalogy [Internet]. 2021 [cited 2024 Jul 18];102:1342–52. Available from:  
501 <https://academic.oup.com/jmammal/article/102/5/1342/6327749>
- 502 15. Melin M, Matala J, Mehtätalo L, Pusenius J, Packalen T. The effect of snow depth on  
503 movement rates of GPS-collared moose. European Journal of Wildlife Research [Internet].  
504 2023 [cited 2023 Jul 20];69:21. Available from: <https://link.springer.com/10.1007/s10344-023-01650-w>
- 505 16. Hetem RS, Fuller A, Maloney SK, Mitchell D. Responses of large mammals to climate  
506 change. Temperature [Internet]. 2014 [cited 2024 Aug 8];1:115–27. Available from: <https://www.tandfonline.com/doi/full/10.4161/temp.29651>
- 507 17. Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR. The travel speeds of large animals  
508 are limited by their heat-dissipation capacities. Hedenstrom A, editor. PLOS Biology  
509 [Internet]. 2023 [cited 2024 Jun 10];21:e3001820. Available from: <https://dx.plos.org/10.1371/journal.pbio.3001820>
- 510 18. Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM. Fine-  
511 grain modeling of species' response to climate change: Holdouts, stepping-stones, and  
512 microrefugia. Trends in Ecology & Evolution [Internet]. 2014 [cited 2025 May 9];29:390–  
513 7. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534714001001>
- 514 19. Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, et al.  
515 Implications of the thermal environment for terrestrial wildlife management. Wildlife  
516 Society Bulletin [Internet]. 2017 [cited 2024 Aug 8];41:183–93. Available from: <https://wildlife.onlinelibrary.wiley.com/doi/10.1002/wsb.772>
- 517 20. Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G. Effects of air temperature  
518 on habitat selection and activity patterns of two tropical imperfect homeotherms. An-  
519 imal Behaviour [Internet]. 2018 [cited 2024 Jun 10];140:129–40. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347218301209>
- 520
- 521
- 522
- 523
- 524

- 525 21. Arechavala-Lopez P, Minguito-Frutos M, Follana-Berná G, Palmer M. Common octopus  
526 settled in human-altered Mediterranean coastal waters: From individual home range to  
527 population dynamics. Durif C, editor. ICES Journal of Marine Science [Internet]. 2019  
528 [cited 2022 Nov 7];76:585–97. Available from: <https://academic.oup.com/icesjms/article/76/2/585/4917675>
- 530 22. Gulland FMD, Baker JD, Howe M, LaBrecque E, Leach L, Moore SE, et al. A review  
531 of climate change effects on marine mammals in United States waters: Past predictions,  
532 observed impacts, current research and conservation imperatives. Climate Change Ecology  
533 [Internet]. 2022 [cited 2025 May 9];3:100054. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2666900522000077>
- 535 23. Hall LE, Chalfoun AD, Beever EA, Loosen AE. Microrefuges and the occurrence of  
536 thermal specialists: Implications for wildlife persistence amidst changing temperatures.  
537 Climate Change Responses [Internet]. 2016 [cited 2025 May 9];3:8. Available from: <http://climatechangeresponses.biomedcentral.com/articles/10.1186/s40665-016-0021-4>
- 539 24. Hegel TM, Mysterud A, Huettmann F, Stenseth NC. Interacting effect of wolves and  
540 climate on recruitment in a northern mountain caribou population. Oikos [Internet]. 2010  
541 [cited 2024 Aug 8];119:1453–61. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1600-0706.2010.18358.x>
- 543 25. Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, et al.  
544 Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society  
545 B: Biological Sciences [Internet]. 2016 [cited 2024 Feb 14];283:20160456. Available from:  
546 <https://royalsocietypublishing.org/doi/10.1098/rspb.2016.0456>
- 547 26. Alston JM, Joyce MJ, Merkle JA, Moen RA. Temperature shapes movement and habitat  
548 selection by a heat-sensitive ungulate. Landscape Ecology [Internet]. 2020 [cited 2022 Nov  
549 18];35:1961–73. Available from: <https://link.springer.com/10.1007/s10980-020-01072-y>
- 550 27. Giroux A, Ortega Z, Attias N, Desbiez ALJ, Valle D, Börger L, et al. Activity modulation  
551 and selection for forests help giant anteaters to cope with temperature changes. Animal

- 552 Behaviour [Internet]. 2023 [cited 2024 Jun 10];201:191–209. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S000334722300101X>
- 553
- 554 28. Mezzini S, Fleming CH, Medici EP, Noonan MJ. How resource abundance and resource  
555 stochasticity affect organisms' range sizes. Movement Ecology [Internet]. 2025 [cited  
556 2025 May 7];13:20. Available from: <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-025-00546-5>
- 557
- 558 29. Martinez-Garcia R, Fleming CH, Seppelt R, Fagan WF, Calabrese JM. How range  
559 residency and long-range perception change encounter rates. Journal of Theoretical Biol-  
560 ogy [Internet]. 2020 [cited 2024 May 30];498:110267. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0022519320301223>
- 561
- 562 30. Weststrate DK, Chhen A, Mezzini S, Safford K, Noonan MJ. How climate change  
563 and population growth will shape attendance and human-wildlife interactions at British  
564 Columbia parks. Journal of Sustainable Tourism [Internet]. 2024 [cited 2024 Apr 12];1–15.  
565 Available from: <https://www.tandfonline.com/doi/full/10.1080/09669582.2024.2331228>
- 566
- 567 31. Wilson RS, Franklin CE, Davison W, Kraft P. Stenotherms at sub-zero temperatures:  
568 Thermal dependence of swimming performance in Antarctic fish. Journal of Compar-  
569 ative Physiology B: Biochemical, Systemic, and Environmental Physiology [Internet].  
570 2001 [cited 2024 Jun 14];171:263–9. Available from: <http://link.springer.com/10.1007/s003600000172>
- 571
- 572 32. Berger J, Hartway C, Gruzdev A, Johnson M. Climate Degradation and Extreme Icing  
573 Events Constrain Life in Cold-Adapted Mammals. Scientific Reports [Internet]. 2018  
574 [cited 2020 Jan 24];8:1156. Available from: <http://www.nature.com/articles/s41598-018-19416-9>
- 575
- 576 33. Dupont L, Thierry M, Zinger L, Legrand D, Jacob S. Beyond reaction norms: The tem-  
577 poral dynamics of phenotypic plasticity. Trends in Ecology & Evolution [Internet]. 2024  
578 [cited 2025 Jan 16];39:41–51. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0169534723002252>

- 579 34. McCain CM. Assessing the risks to United States and Canadian mammals caused by  
580 climate change using a trait-mediated model. Heske E, editor. *Journal of Mammalogy*  
581 [Internet]. 2019 [cited 2024 Jul 18];gyz155. Available from: <https://academic.oup.com/jmammal/advance-article/doi/10.1093/jmammal/gyz155/5614284>
- 582
- 583 35. Polazzo F, Limberger R, Pennekamp F, Ross SRP-J, Simpson GL, Petchey OL. Mea-  
584 suring the Response Diversity of Ecological Communities Experiencing Multifarious Envi-  
585 ronmental Change. *Global Change Biology* [Internet]. 2024 [cited 2025 Jan 16];30:e17594.  
586 Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.17594>
- 587 36. Levins RA. Evolution in changing environments: Some theoretical explorations. 3.  
588 printing. Princeton, NJ: Princeton Univ. Press; 1974.
- 589 37. Xu W, Barker K, Shawler A, Van Scyoc A, Smith JA, Mueller T, et al. The plasticity  
590 of ungulate migration in a changing world. *Ecology* [Internet]. 2021 [cited 2025 Jan  
591 16];102:e03293. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3293>
- 592
- 593 38. IPCC. Climate Change 2021 – The Physical Science Basis: Working Group I Contribu-  
594 tion to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change  
595 [Internet]. 1st ed. Cambridge University Press; 2023 [cited 2023 Jun 30]. Available from:  
596 <https://www.cambridge.org/core/product/identifier/9781009157896/type/book>
- 597 39. Zurowski M. The summer Canada burned: The wildfire season that shocked the world.  
598 Vancouver: Postmedia / Greystone Books; 2023.
- 599 40. Deb JC, Forbes G, MacLean DA. Modelling the spatial distribution of selected North  
600 American woodland mammals under future climate scenarios. *Mammal Review* [Internet].  
601 2020 [cited 2024 Jun 13];50:440–52. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/mam.12210>
- 602
- 603 41. Woo-Durand C, Matte J-M, Cuddihy G, McGourdji CL, Venter O, Grant JWA. In-  
604 creasing importance of climate change and other threats to at-risk species in Canada.  
605 *Environmental Reviews* [Internet]. 2020 [cited 2022 Jun 23];28:449–56. Available from:

- 606      <https://cdnsciencepub.com/doi/10.1139/er-2020-0032>
- 607    42. Bunnell FL, Kremsater LL, Wells RW. Global Weirding in British Columbia: Climate  
608       Change and the Habitat of Terrestrial Vertebrates. *Journal of Ecosystems and Manage-  
609       ment* [Internet]. 2011 [cited 2024 Jun 14];12. Available from: <https://jem-online.org/index.php/jem/article/view/74>
- 610
- 611    43. Sih A, Ferrari MCO, Harris DJ. Evolution and behavioural responses to human-induced  
612       rapid environmental change: Behaviour and evolution. *Evolutionary Applications* [Inter-  
613       net]. 2011 [cited 2022 Oct 5];4:367–87. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1752-4571.2010.00166.x>
- 614
- 615    44. Sawyer H, Kauffman MJ, Nielson RM, Horne JS. Identifying and prioritizing ungulate  
616       migration routes for landscape-level conservation. *Ecological Applications* [Internet]. 2009  
617       [cited 2025 Jan 16];19:2016–25. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-2034.1>
- 618
- 619    45. Verzuh TL, Rogers SA, Mathewson PD, May A, Porter WP, Class C, et al. Behavioural  
620       responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales.  
621       *Journal of Animal Ecology* [Internet]. 2023 [cited 2024 Jun 12];92:619–34. Available from:  
622       <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13873>
- 623
- 624    46. Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL. Migratory plas-  
625       ticity is not ubiquitous among large herbivores. Chapman J, editor. *Journal of An-  
626       imal Ecology* [Internet]. 2019 [cited 2025 Jan 16];88:450–60. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12926>
- 627
- 628    47. Botero CA, Weissing FJ, Wright J, Rubenstein DR. Evolutionary tipping points in  
the capacity to adapt to environmental change. *Proceedings of the National Academy of  
629       Sciences* [Internet]. 2015 [cited 2025 Feb 24];112:184–9. Available from: <https://pnas.org/doi/full/10.1073/pnas.1408589111>
- 630
- 631    48. Sherwood SC, Huber M. An adaptability limit to climate change due to heat stress.  
632       *Proceedings of the National Academy of Sciences* [Internet]. 2010 [cited 2024 Jun

- 633 14];107:9552–5. Available from: <https://pnas.org/doi/full/10.1073/pnas.0913352107>
- 634 49. Williams JE, Blois JL. Range shifts in response to past and future climate change: Can  
635 climate velocities and species' dispersal capabilities explain variation in mammalian range  
636 shifts? *Journal of Biogeography* [Internet]. 2018 [cited 2024 Jul 18];45:2175–89. Available  
637 from: <https://onlinelibrary.wiley.com/doi/10.1111/jbi.13395>
- 638 50. Mota-Rojas D, Titto CG, Orihuela A, Martínez-Burnes J, Gómez-Prado J, Torres-Bernal  
639 F, et al. Physiological and Behavioral Mechanisms of Thermoregulation in Mammals.  
640 Animals [Internet]. 2021 [cited 2024 Jun 12];11:1733. Available from: <https://www.mdpi.com/2076-2615/11/6/1733>
- 642 51. Dierauer JR, Allen DM, Whitfield PH. Climate change impacts on snow and stream-  
643 flow drought regimes in four ecoregions of British Columbia. *Canadian Water Resources  
644 Journal / Revue canadienne des ressources hydriques* [Internet]. 2021 [cited 2025 Jan  
645 16];46:168–93. Available from: <https://www.tandfonline.com/doi/full/10.1080/07011784.2021.1960894>
- 647 52. Turner NJ, Clifton H. "It's so different today": Climate change and indigenous life-  
648 ways in British Columbia, Canada. *Global Environmental Change* [Internet]. 2009 [cited  
649 2025 Feb 20];19:180–90. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0959378009000223>
- 651 53. Tysor CS. Countergradient variation in lodgepole pine flowering phenology. 2025 [cited  
652 2025 Feb 20]; Available from: <https://doi.library.ubc.ca/10.14288/1.0447901>
- 653 54. Basu A, Culpepper J, Blagrave K, Sharma S. Phenological Shifts in Lake Ice Cover  
654 Across the Northern Hemisphere: A Glimpse Into the Past, Present, and the Future  
655 of Lake Ice Phenology. *Water Resources Research* [Internet]. 2024 [cited 2025 Feb  
656 20];60:e2023WR036392. Available from: <https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2023WR036392>
- 658 55. Zhang X, Zhou T, Zhang W, Ren L, Jiang J, Hu S, et al. Increased impact of heat  
659 domes on 2021-like heat extremes in North America under global warming. *Nature*

- 660      Communications [Internet]. 2023 [cited 2025 Jan 21];14:1690. Available from: <https://www.nature.com/articles/s41467-023-37309-y>
- 661
- 662      56. Convention on Biological Diversity. 15/4. Kunming-Montreal Global Biodiversity Framework [Internet]. 2022 [cited 2025 Jan 16]. Available from: <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>
- 663
- 664      57. Riahi K, Vuuren DP van, Kriegler E, Edmonds J, O'Neill BC, Fujimori S, et al. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Global Environmental Change [Internet]. 2017 [cited 2023 Mar 21];42:153–68. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0959378016300681>
- 665
- 666
- 667
- 668
- 669
- 670      58. Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B: Biological Sciences [Internet]. 2012 [cited 2024 Jun 13];279:4407–16. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2012.1483>
- 671
- 672
- 673
- 674      59. Kays R, Davidson SC, Berger M, Bohrer G, Fiedler W, Flack A, et al. The Movebank system for studying global animal movement and demography. Methods in Ecology and Evolution [Internet]. 2022 [cited 2022 Mar 3];13:419–31. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.13767>
- 675
- 676
- 677
- 678      60. Hersbach H, Bell B, Berrisford P, Biavati G, Horányi A, Muñoz Sabater J, et al. ERA5 hourly data on single levels from 1940 to present [Internet]. Copernicus Climate Change Service (C3S) Climate Data Store (CDS); 2023 [cited 2024 Mar 27]. Available from: <https://cds.climate.copernicus.eu/doi/10.24381/cds.adbb2d47>
- 679
- 680
- 681
- 682      61. Hijmans RJ. Terra: Spatial Data Analysis [Internet]. 2023. Available from: <https://CRAN.R-project.org/package=terra>
- 683
- 684      62. R Core Team. R: A Language and Environment for Statistical Computing [Internet].
- 685      Vienna, Austria: R Foundation for Statistical Computing; 2024. Available from: <https://www.R-project.org/>
- 686

63. Burnett M. *climatenaR*: Tools to Access ClimateNA data. 2023.

64. Rigby RA, Stasinopoulos DM. Generalized additive models for location, scale and shape (with discussion). *Journal of the Royal Statistical Society: Series C (Applied Statistics)* [Internet]. 2005 [cited 2022 Jun 26];54:507–54. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1467-9876.2005.00510.x>

65. Stasinopoulos MD, Rigby RA. Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software*. 2007;23.

66. Wood SN. Generalized additive models: An introduction with R. Second edition. Boca Raton: CRC Press/Taylor & Francis Group; 2017.

67. Tuanmu M, Jetz W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography* [Internet]. 2014 [cited 2025 Jan 17];23:1031–45. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/geb.12182>

68. Hollister J, Shah T, Nowosad J, Robitaille AL, Beck MW, Johnson M. Elevatr: Access Elevation Data from Various APIs [Internet]. 2023. Available from: <https://github.com/jhollist/elevatr/>

69. Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales. *The American Naturalist* [Internet]. 2014 [cited 2022 Jul 26];183:E154–67. Available from: <https://www.journals.uchicago.edu/doi/10.1086/675504>

70. Fleming CH, Calabrese JM. Ctmm: Continuous-Time Movement Modeling [Internet]. 2023. Available from: <https://CRAN.R-project.org/package=ctmm>

71. Noonan MJ, Fleming CH, Akre TS, Drescher-Lehman J, Gurarie E, Harrison A-L, et al. Scale-insensitive estimation of speed and distance traveled from animal tracking data. *Movement Ecology* [Internet]. 2019 [cited 2021 Jun 23];7:35. Available from: <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-019-0177-1>

72. Matthiopoulos J. Defining, estimating, and understanding the fundamental niches of

- 714 complex animals in heterogeneous environments. Ecological Monographs [Internet]. 2022  
715 [cited 2025 Jan 17];92:e1545. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecm.1545>
- 716
- 717 73. Pedersen EJ, Miller DL, Simpson GL, Ross N. Hierarchical generalized additive models  
718 in ecology: An introduction with mgcv. PeerJ [Internet]. 2019 [cited 2020 Jan 24];7:e6876.  
719 Available from: <https://peerj.com/articles/6876>
- 720 74. Wood SN, Goude Y, Shaw S. Generalized additive models for large data sets. Journal of  
721 the Royal Statistical Society: Series C (Applied Statistics) [Internet]. 2015 [cited 2022 Mar  
722 11];64:139–55. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/rssc.12068>
- 723 75. Wood SN, Li Z, Shaddick G, Augustin NH. Generalized Additive Models for Gigadata:  
724 Modeling the U.K. Black Smoke Network Daily Data. Journal of the American Statistical  
725 Association [Internet]. 2017 [cited 2022 Mar 11];112:1199–210. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1195744>
- 726
- 727 76. Li Z, Wood SN. Faster model matrix crossproducts for large generalized linear models  
728 with discretized covariates. Statistics and Computing [Internet]. 2020;30:19–25. Available  
729 from: <https://doi.org/10.1007/s11222-019-09864-2>
- 730 77. Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J. Estimating space-use  
731 and habitat preference from wildlife telemetry data. Ecography [Internet]. 2008 [cited  
732 2023 Jun 22];31:140–60. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.2007.0906-7590.05236.x>
- 733
- 734 78. Fleming CH, Calabrese JM. A new kernel density estimator for accurate home-range and  
735 species-range area estimation. Dray S, editor. Methods in Ecology and Evolution [Inter-  
736 net]. 2017 [cited 2025 Jan 17];8:571–9. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.12673>
- 737
- 738 79. Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, et al. A comprehen-  
739 sive analysis of autocorrelation and bias in home range estimation. Ecological Monographs  
740 [Internet]. 2019 [cited 2020 Oct 23];89:e01344. Available from: <https://onlinelibrary.wiley.com/doi/10.1002/ecm.1344>

- 741      [com/doi/abs/10.1002/ecm.1344](https://doi/abs/10.1002/ecm.1344)
- 742    80. Johnson DH. The Comparison of Usage and Availability Measurements for Evaluating  
743       Resource Preference. *Ecology* [Internet]. 1980 [cited 2025 Jan 17];61:65–71. Available  
744       from: <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1937156>
- 745    81. Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, et al. Mitigating  
746       pseudoreplication and bias in resource selection functions with autocorrelation-informed  
747       weighting. *Methods in Ecology and Evolution* [Internet]. 2022 [cited 2022 Dec  
748       12];2041–210X.14025. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.14025>
- 750    82. Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, et al. Emergence of  
751       universal scaling in weather extreme events. 2022 [cited 2022 Nov 20]; Available from:  
752       <https://arxiv.org/abs/2209.02292>
- 753    83. Logares R, Nuñez M. Black Swans in ecology and evolution: The importance of improb-  
754       able but highly influential events. *Ideas in Ecology and Evolution* [Internet]. 2012 [cited  
755       2020 Feb 12]; Available from: <https://ojs.library.queensu.ca/index.php/IEE/article/view/4311>
- 756    84. Anderson SC, Branch TA, Cooper AB, Dulvy NK. Black-swan events in animal  
757       populations. *Proceedings of the National Academy of Sciences* [Internet]. 2017 [cited  
758       2020 Jan 24];114:3252–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1611525114>
- 761    85. Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM. Life history consequences of  
762       climate change in hibernating mammals: A review. *Ecography* [Internet]. 2022 [cited  
763       2025 Jan 21];2022:e06056. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.06056>
- 765    86. Mortlock E, Silovský V, Güldenpfennig J, Faltusová M, Olejarz A, Börger L, et al. Sleep  
766       in the wild: The importance of individual effects and environmental conditions on sleep  
767       behaviour in wild boar. *Proceedings of the Royal Society B: Biological Sciences* [Internet].

- 768 2024 [cited 2025 Jan 21];291:20232115. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2023.2115>
- 769
- 770 87. Fjelldal MA, Wright J, Stawski C. Nightly torpor use in response to weather conditions  
771 and individual state in an insectivorous bat. *Oecologia* [Internet]. 2021 [cited 2022 Oct  
772 3];197:129–42. Available from: <https://link.springer.com/10.1007/s00442-021-05022-6>
- 773 88. Johnson HE, Lewis DL, Verzuh TL, Wallace CF, Much RM, Willmarth LK, et al.  
774 Human development and climate affect hibernation in a large carnivore with implications  
775 for human–carnivore conflicts. Bieber C, editor. *Journal of Applied Ecology* [Internet].  
776 2018 [cited 2025 Jan 21];55:663–72. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.13021>
- 777
- 778 89. Schmidt NM, Grøndahl C, Evans AL, Desforges J-P, Blake J, Hansen LH, et al. On  
779 the interplay between hypothermia and reproduction in a high arctic ungulate. *Scientific  
780 Reports* [Internet]. 2020 [cited 2022 Sep 2];10:1514. Available from: <http://www.nature.com/articles/s41598-020-58298-8>
- 781
- 782 90. Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D. Cold and hungry: Combined  
783 effects of low temperature and resource scarcity on an edge-of-range temperate primate,  
784 the golden snub-nose monkey. *Ecography* [Internet]. 2020 [cited 2022 Oct 3];43:1672–82.  
785 Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.05295>
- 786
- 787 91. Gilbert SL, Hundertmark KJ, Person DK, Lindberg MS, Boyce MS. Behavioral  
788 plasticity in a variable environment: Snow depth and habitat interactions drive  
789 deer movement in winter. *Journal of Mammalogy* [Internet]. 2017 [cited 2025  
790 Jan 21];98:246–59. Available from: <https://academic.oup.com/jmammal/article-lookup/doi/10.1093/jmammal/gyw167>
- 791
- 792 92. Pedersen SH, Bentzen TW, Reinking AK, Liston GE, Elder K, Lenart EA, et al.  
793 Quantifying effects of snow depth on caribou winter range selection and movement in  
794 Arctic Alaska. *Movement Ecology* [Internet]. 2021 [cited 2025 Jan 21];9:48. Available  
from: <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-021-00462-0>

795 00276-4

- 796 93. Slatyer RA, Umbers KDL, Arnold PA. Ecological responses to variation in seasonal snow  
797 cover. *Conservation Biology* [Internet]. 2022 [cited 2025 Jan 21];36:e13727. Available from:  
798 <https://onlinelibrary.wiley.com/doi/10.1111/cobi.13727>
- 799 94. Sullender BK, Cunningham CX, Lundquist JD, Prugh LR. Defining the danger zone:  
800 Critical snow properties for predator-prey interactions. *Oikos* [Internet]. 2023 [cited  
801 2025 Jan 21];2023:e09925. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.09925>
- 802 95. Aven T, Kvaløy JT. Implementing the Bayesian paradigm in risk analysis. *Reliability  
Engineering & System Safety* [Internet]. 2002 [cited 2025 Jan 30];78:195–201. Available  
803 from: <https://linkinghub.elsevier.com/retrieve/pii/S0951832002001618>
- 804 96. Ayre KK, Landis WG. A Bayesian Approach to Landscape Ecological Risk Assessment  
805 Applied to the Upper Grande Ronde Watershed, Oregon. *Human and Ecological Risk  
Assessment: An International Journal* [Internet]. 2012 [cited 2025 Jan 30];18:946–70.  
806 Available from: <http://www.tandfonline.com/doi/abs/10.1080/10807039.2012.707925>
- 807 97. Czado C, Brechmann EC. Bayesian Risk Analysis. In: Klüppelberg C, Straub D,  
808 Welpe IM, editors. *Risk - A Multidisciplinary Introduction* [Internet]. Cham: Springer  
809 International Publishing; 2014 [cited 2025 Jan 30]. p. 207–40. Available from: [https://link.springer.com/10.1007/978-3-319-04486-6\\_8](https://link.springer.com/10.1007/978-3-319-04486-6_8)
- 810 98. McNutt M, Hildebrand J. Scientists in the line of fire. *Science* [Internet]. 2022 [cited  
811 2025 Feb 11];375:1071–1. Available from: <https://www.science.org/doi/10.1126/science.abp8817>
- 812 99. Tollefson J. What the war in Ukraine means for energy, climate and food. *Nature*  
813 [Internet]. 2022 [cited 2025 Feb 11];604:232–3. Available from: <https://www.nature.com/articles/d41586-022-00969-9>
- 814 100. Roumeliotis KI, Tsaklikas ND. ChatGPT and Open-AI Models: A Preliminary Review.  
815 Future Internet [Internet]. 2023 [cited 2025 Feb 11];15:192. Available from: [https://www.](https://www.816)

- 822 [mdpi.com/1999-5903/15/6/192](https://mdpi.com/1999-5903/15/6/192)
- 823 101. Van Noorden R, Webb R. ChatGPT and science: The AI system was a force in 2023 —  
824 for good and bad. *Nature* [Internet]. 2023 [cited 2025 Feb 11];624:509–9. Available from:  
825 <https://www.nature.com/articles/d41586-023-03930-6>
- 826 102. DeepSeek-AI, Guo D, Yang D, Zhang H, Song J, Zhang R, et al. DeepSeek-R1:  
827 Incentivizing Reasoning Capability in LLMs via Reinforcement Learning [Internet]. arXiv;  
828 2025 [cited 2025 Jan 30]. Available from: <https://arxiv.org/abs/2501.12948>
- 829 103. Li P, Yang J, Islam MA, Ren S. Making AI Less "Thirsty": Uncovering and Addressing  
830 the Secret Water Footprint of AI Models [Internet]. arXiv; 2023 [cited 2025 Jan 16].  
831 Available from: <https://arxiv.org/abs/2304.03271>
- 832 104. Luccioni AS, Viguier S, Ligozat A-L. Estimating the carbon footprint of BLOOM, a  
833 176B parameter language model. *J Mach Learn Res.* 2024;24.
- 834 105. United Nations Environment Programme, Olhoff A, Bataille C, Christensen J, Den  
835 Elzen M, Fransen T, et al. Emissions Gap Report 2024: No more hot air ... please! With  
836 a massive gap between rhetoric and reality, countries draft new climate commitments  
837 [Internet]. United Nations Environment Programme; 2024 [cited 2025 Jan 30]. Available  
838 from: <https://wedocs.unep.org/20.500.11822/46404>
- 839 106. Huang M-T, Zhai P-M. Achieving Paris Agreement temperature goals requires carbon  
840 neutrality by middle century with far-reaching transitions in the whole society. *Advances*  
841 in Climate Change Research [Internet]. 2021 [cited 2025 Jan 30];12:281–6. Available from:  
842 <https://linkinghub.elsevier.com/retrieve/pii/S1674927821000435>
- 843 107. Simmons BA, Nolte C, McGowan J. Tough questions for the “30 × 30” conserva-  
844 tion agenda. *Frontiers in Ecology and the Environment* [Internet]. 2021 [cited 2025 Feb  
845 11];19:322–3. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2375>
- 847 108. Guenette JD, Kenworthy PG, Wheeler CM. Implications of the War in Ukraine for  
848 the Global Economy.<http://documents.worldbank.org/curated/en/099616504292238906>.

- 849 Washington, D.C.: World Bank Group; 2022 Mar. Report No.: 3.
- 850 109. Sovacool BK, Baum C, Low S. The next climate war? Statecraft, security, and  
851 weaponization in the geopolitics of a low-carbon future. Energy Strategy Reviews [In-  
852 ternet]. 2023 [cited 2025 Feb 18];45:101031. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2211467X22002255>
- 853 110. Wong C, Ballegooien K, Ignace L, Johnson MJ(Gùdia), Swanson H. Towards rec-  
854 onciliation: 10 Calls to Action to natural scientists working in Canada. Boran I, ed-  
855 itor. FACETS [Internet]. 2020 [cited 2021 Oct 27];5:769–83. Available from: <http://www.facetsjournal.com/doi/10.1139/facets-2020-0005>
- 856 111. Lamb CT, Willson R, Menzies AK, Owens-Beek N, Price M, McNay S, et al. Braiding  
857 Indigenous rights and endangered species law. Science [Internet]. 2023 [cited 2023 Jul  
858 19];380:694–6. Available from: <https://www.science.org/doi/10.1126/science.adg9830>
- 859 112. Cunningham SJ, Gardner JL, Martin RO. Opportunity costs and the response of birds  
860 and mammals to climate warming. Frontiers in Ecology and the Environment [Internet].  
861 2021 [cited 2025 Jan 30];19:300–7. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2324>
- 862 113. Glass TW, Breed GA, Robards MD, Williams CT, Kielland K. Trade-off between pre-  
863 dation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted  
864 mesocarnivore. Animal Behaviour [Internet]. 2021 [cited 2025 Jan 30];175:163–74. Avail-  
865 able from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347221000658>
- 866 114. Brivio F, Apollonio M, Anderwald P, Filli F, Bassano B, Bertolucci C, et al. Seek-  
867 ing temporal refugia to heat stress: Increasing nocturnal activity despite predation risk.  
868 Proceedings of the Royal Society B: Biological Sciences [Internet]. 2024 [cited 2025 Jan  
869 30];291:20231587. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2023.1587>
- 870 115. Carbeck K, Wang T, Reid JM, Arcese P. Adaptation to climate change through seasonal  
871 migration revealed by climatic versus demographic niche models. Global Change Biology  
872
- 873 2023.1587
- 874 115. Carbeck K, Wang T, Reid JM, Arcese P. Adaptation to climate change through seasonal  
875 migration revealed by climatic versus demographic niche models. Global Change Biology

- 876 [Internet]. 2022 [cited 2025 Feb 24];28:4260–75. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.16185>
- 877
- 878 116. Morley ID. Spatiotemporal analysis of ecosystem change and landscape connectivity  
879 using satellite imagery in west-central British Columbia, Canada. 2021 [cited 2025 Feb  
880 24]; Available from: <https://doi.library.ubc.ca/10.14288/1.0402358>
- 881 117. Malpeli KC. Ungulate migration in a changing climate—An initial assessment of climate  
882 impacts, management priorities, and science needs [Internet]. Reston, VA; 2022 p. 32.  
883 Report No.: 1493. Available from: <https://pubs.usgs.gov/publication/cir1493>
- 884 118. McLellan ML, McLellan BN. Effect of Season and High Ambient Temperature on  
885 Activity Levels and Patterns of Grizzly Bears (*Ursus arctos*). Crocker DE, editor. PLOS  
886 ONE [Internet]. 2015 [cited 2025 Mar 3];10:e0117734. Available from: <https://dx.plos.org/10.1371/journal.pone.0117734>
- 887
- 888 119. Pigeon KE, Stenhouse G, Côté SD. Drivers of hibernation: Linking food and weather to  
889 denning behaviour of grizzly bears. Behavioral Ecology and Sociobiology [Internet]. 2016  
890 [cited 2025 Mar 3];70:1745–54. Available from: <http://link.springer.com/10.1007/s00265-016-2180-5>
- 891
- 892 120. Liu JA, Meléndez-Fernández OH, Bumgarner JR, Nelson RJ. Effects of light pollu-  
893 tion on photoperiod-driven seasonality. Hormones and Behavior [Internet]. 2022 [cited  
894 2025 Feb 24];141:105150. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0018506X22000447>
- 895
- 896 121. Xu F, Si Y. The frost wave hypothesis: How the environment drives autumn departure of  
897 migratory waterfowl. Ecological Indicators [Internet]. 2019 [cited 2025 Feb 24];101:1018–  
898 25. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S1470160X19301335>
- 899
- 900 122. Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, et al. Green-wave surfing increases fat gain in a migratory ungulate. Oikos [Internet]. 2018  
901 [cited 2022 Sep 2];127:1060–8. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.05227>
- 902

- 903 123. Wright CA. Survival and movements of mule deer (*Odocoileus hemionus*) in southern  
904 British Columbia [Internet] [{PhD} {Thesis}]. University of British Columbia; 2024.  
905 Available from: <https://open.library.ubc.ca/collections/ubctheses/24/items/1.0441418>
- 906 124. Zuñiga-Palacios J, Zuria I, Castellanos I, Lara C, Sánchez-Rojas G. What do we know  
907 (and need to know) about the role of urban habitats as ecological traps? Systematic  
908 review and meta-analysis. *Science of The Total Environment* [Internet]. 2021 [cited  
909 2025 Feb 24];780:146559. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0048969721016272>
- 910 125. Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R. An overview of eco-  
911 logical traps in marine ecosystems. *Frontiers in Ecology and the Environment* [Internet].  
912 2021 [cited 2025 Feb 24];19:234–42. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2322>
- 913 126. Environment and Climate Change Canada. Canadian Environmental Sustainability  
914 Indicators: Canada's conserved areas. [Internet]. 2024. Available from:  
915 [www.canada.ca/en/environment-climate-change/services/environmental-indicators/conserved-areas.html](https://www.canada.ca/en/environment-climate-change/services/environmental-indicators/conserved-areas.html)
- 916 127. Minister of Environment and Climate Change. An Act respecting transparency and  
917 accountability in relation to certain commitments Canada has made under the Convention  
918 on Biological Diversity [Internet]. 2024 [cited 2025 Feb 24]. Available from: <https://www.parl.ca/legisinfo/en/bill/44-1/c-73>
- 919 128. Falardeau M, Bennett EM, Else B, Fisk A, Mundy CJ, Choy ES, et al. Biophysical  
920 indicators and Indigenous and Local Knowledge reveal climatic and ecological shifts with  
921 implications for Arctic Char fisheries. *Global Environmental Change* [Internet]. 2022  
922 [cited 2025 Feb 24];74:102469. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0959378022000073>
- 923 129. Desjardins SPA, Friesen TM, Jordan PD. Looking back while moving forward: How  
924 past responses to climate change can inform future adaptation and mitigation strategies

- 930       in the Arctic. *Quaternary International* [Internet]. 2020 [cited 2025 Feb 24];549:239–48.
- 931       Available from: <https://linkinghub.elsevier.com/retrieve/pii/S1040618220302822>
- 932       130. Hessami MA, Bowles E, Popp JN, Ford AT. Indigenizing the North American Model  
933       of Wildlife Conservation. Beazley K, editor. *FACETS* [Internet]. 2021 [cited 2021 Nov  
934       4];6:1285–306. Available from: <https://facetsjournal.com/doi/10.1139/facets-2020-0088>
- 935       131. Smith BJ, MacNulty DR, Stahler DR, Smith DW, Avgar T. Density-dependent habitat  
936       selection alters drivers of population distribution in northern Yellowstone elk. *Ecology Letters*  
937       [Internet]. 2023 [cited 2025 May 9];26:245–56. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.14155>
- 938
- 939       132. Tórrez-Herrera LL, Davis GH, Crofoot MC. Do Monkeys Avoid Areas of Home Range  
940       Overlap Because They Are Dangerous? A Test of the Risk Hypothesis in White-Faced  
941       Capuchin Monkeys (*Cebus capucinus*). *International Journal of Primatology* [Internet].  
942       2020 [cited 2022 Mar 9];41:246–64. Available from: <http://link.springer.com/10.1007/s10764-019-00110-0>
- 943
- 944       133. Kohl MT, Ruth TK, Metz MC, Stahler DR, Smith DW, White PJ, et al. Do prey  
945       select for vacant hunting domains to minimize a multi-predator threat? Gaillard J, editor.  
946       *Ecology Letters* [Internet]. 2019 [cited 2025 Jan 20];22:1724–33. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.13319>
- 947
- 948       134. Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, et  
949       al. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements.  
950       *Science* [Internet]. 2018 [cited 2020 Nov 11];359:466–9. Available from: <https://www.sciencemag.org/lookup/doi/10.1126/science.aam9712>
- 951
- 952       135. Rosenthal J, Booth R, Carolan N, Clarke O, Curnew J, Hammond C, et al. The impact  
953       of recreational activities on species at risk in Canada. *Journal of Outdoor Recreation  
954       and Tourism* [Internet]. 2022 [cited 2025 Feb 24];40:100567. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2213078022000895>
- 955
- 956       136. Rice WL. The conspicuous consumption of wilderness, or leisure lost in the wilderness.

- 957 World Leisure Journal [Internet]. 2022 [cited 2025 Feb 24];64:451–68. Available from:  
958 <https://www.tandfonline.com/doi/full/10.1080/16078055.2022.2096109>
- 959 137. Duncan C, Chauvenet ALM, McRae LM, Pettorelli N. Predicting the Future Impact  
960 of Droughts on Ungulate Populations in Arid and Semi-Arid Environments. Seebacher  
961 F, editor. PLoS ONE [Internet]. 2012 [cited 2025 Feb 24];7:e51490. Available from:  
962 <https://dx.plos.org/10.1371/journal.pone.0051490>
- 963 138. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data ap-  
964 proaches lead to an increased understanding of the ecology of animal movement. Science  
965 [Internet]. 2022 [cited 2022 Mar 9];375:eabg1780. Available from: <https://www.science.org/doi/10.1126/science.abg1780>
- 966 139. Pease BS. Ecological scales of effect vary across space and time. Ecography [Internet].  
967 2024 [cited 2024 Aug 8];2024:e07163. Available from: <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.07163>
- 969 140. Steixner-Kumar S, Gläscher J. Strategies for navigating a dynamic world. Science  
970 [Internet]. 2020 [cited 2022 Mar 9];369:1056–7. Available from: <https://www.science.org/doi/10.1126/science.abd7258>
- 972 141. McElreath R. Statistical rethinking: A Bayesian course with examples in R and Stan.  
973 Second edition. Boca Raton London New York: CRC Press; 2020.