

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

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

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

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

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

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

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

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

⁵ BC Parks

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

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

Article type: Research article

Words in abstract: 242

Words in main text: 6349

Figures: 7

Tables: 3

References: 142 (updated on 2025-05-09)

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 research has quantified the effects of temperature on mammalian movement behaviour, but few have quantified the effects of future climate change on mammalian movement. Consequently, it is still unclear how and where mammals will move in the 21st 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 21st century. We found no common effects of temperature on the species' movement rates, so we suggest that estimated responses be considered 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 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.

¹ 1 Introduction

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

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

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

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

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

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

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

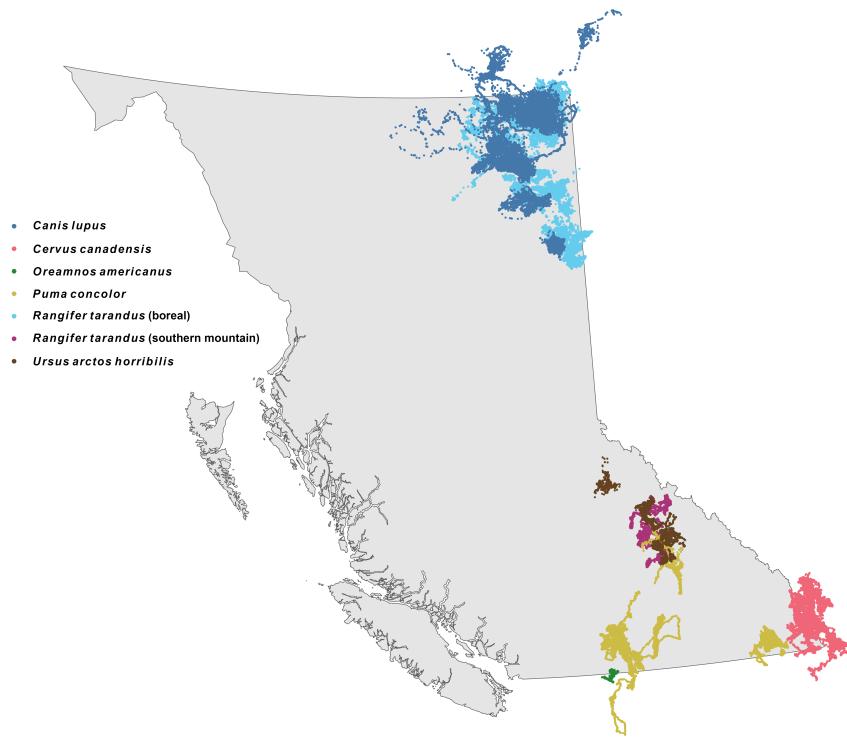


Figure 1: GPS telemetry data for the six species in this study.

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

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

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

62 2 Methods

63 2.1 Datasets used

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

70 2.1.1 GPS telemetry data

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

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

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

82 **2.1.2 Historical and projected temperature data**

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

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

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

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

110 2.1.3 Resource rasters

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

123 2.2 Estimating mammals' instantaneous speeds

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

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

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

2.3 Estimating the effects of temperature on mammals' movement

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

2.3.1 Disentangling direct and indirect effects

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

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

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

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

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

```
m_moving <- bam(
  moving ~
    s(animal, bs = 're') +
    species + #' necessary since `by` terms do not include intercept terms
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  data = d,
  method = 'fREML', # fast REML
  discrete = TRUE, # discretize the covariates for faster computation
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5))) #' for `bs = 'cc'`

m_speed <- bam(
  speed_est ~
    s(animal, bs = 're') +
    species +
    s(tod_pdt, by = species, k = 5, bs = 'cc') +
    s(doy, by = species, k = 5, bs = 'cc') +
    s(temp_c, by = species, k = 5, bs = 'tp') +
    ti(doy, tod_pdt, by = species, k = 5, bs = c('cc', 'cc')) +
    ti(temp_c, tod_pdt, by = species, k = 5, bs = c('tp', 'cc')) +
    ti(temp_c, doy, by = species, k = 5, bs = c('tp', 'cc')) +
    s(log(dt), k = 3) +
    s(log(dt), species, k = 3, bs = 'fs'),
  family = Gamma(link = 'log'),
  data = d_2, #' data filtered for only moving
  method = 'fREML',
  discrete = TRUE,
  knots = list(tod_pdt = c(0, 1), doy = c(0.5, 366.5)))
```

186 2.3.3 Effects of temperature on habitat selection

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

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

```

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

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

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

213 3 Results

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

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

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

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

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

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

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

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

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

240 3.1 Effects of temperature on movement rates

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

254 3.2 Effects of temperature on habitat selection

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

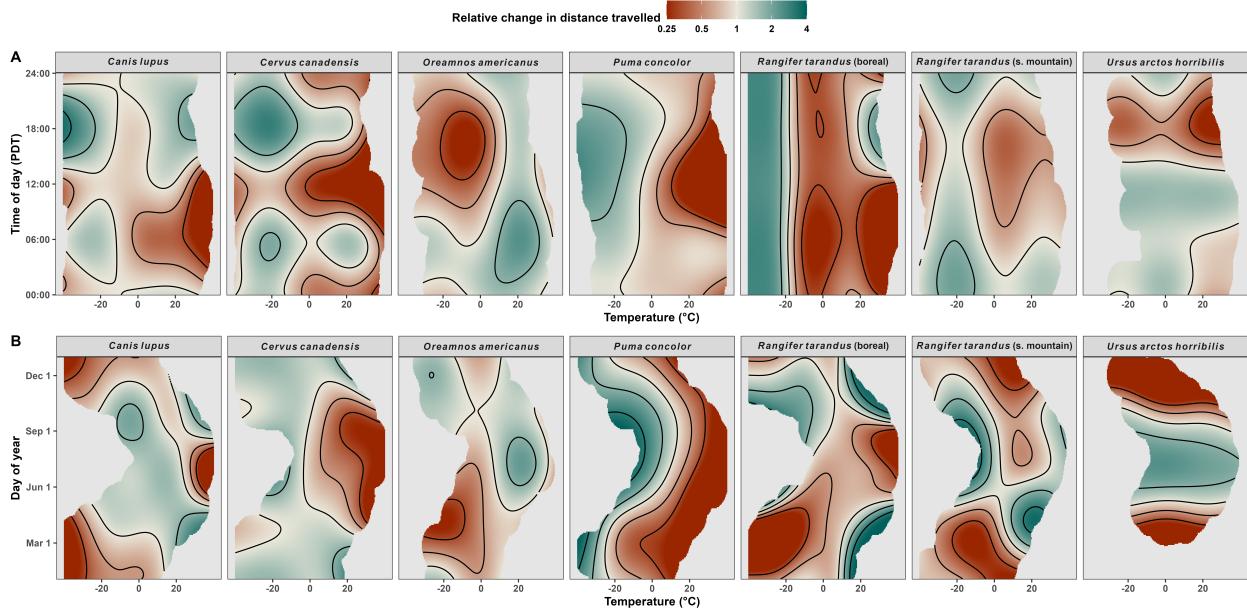


Figure 2: Temperature is a strong determinant of how far and when mammals travel. The fill indicates the estimated effects of temperature on the relative change in distance travelled (probability of moving times mean speed when moving) over time of day on June 1st (**A**) and day of year at 12:00 PDT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

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

269 3.3 Predicted changes in movement during the 21st century

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

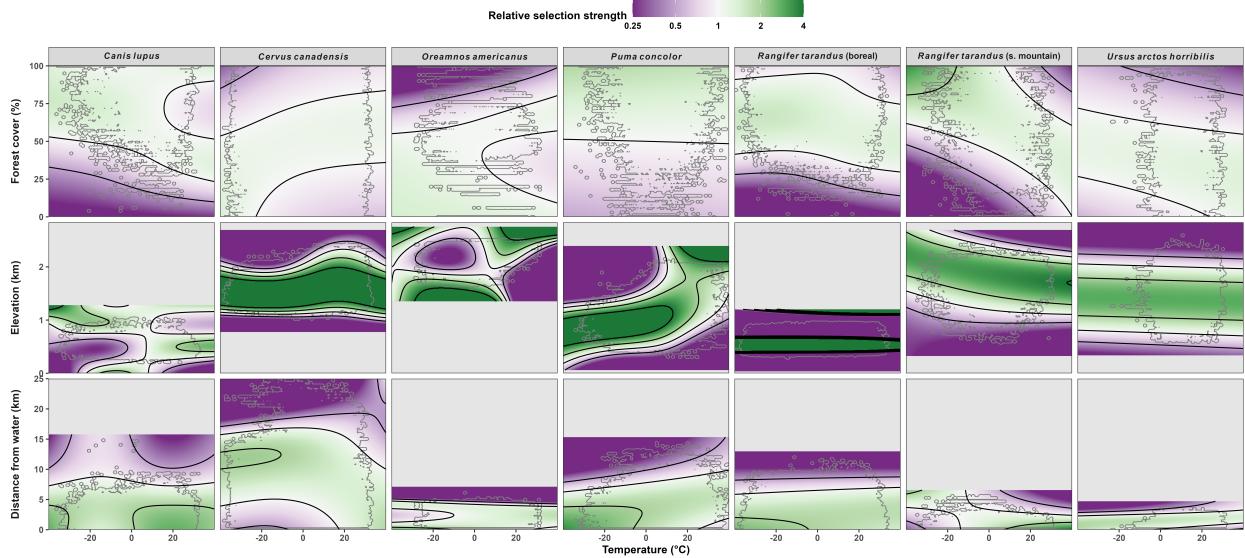


Figure 3: Temperature strongly affects mammals' habitat selection. Estimated relative selection strength (RSS) for forest cover (%), elevation (km), and distance from water (km) as a function of temperature. The grey contours indicate the extent of each species' observed locations. RSS values were re-centered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

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

All species exhibited a decrease in RSS within their current range, irrespective of climate change scenario. Changes were often only between -1% and -3% under the best-case scenario but they ranged from -8% to -14% under the worst-case scenario (6). As with distance traveled, the change in RSS in 2100 varied throughout BC for all species (Fig. 7). All species were predicted to exhibit a decrease in RSS throughout most of BC, with the exception of boreal caribou, which had a predicted increase in approximately 67% of the province, including their current range. The increase was in great part due to the estimated increase in selection for high-elevation areas that are well outside the population's current range.

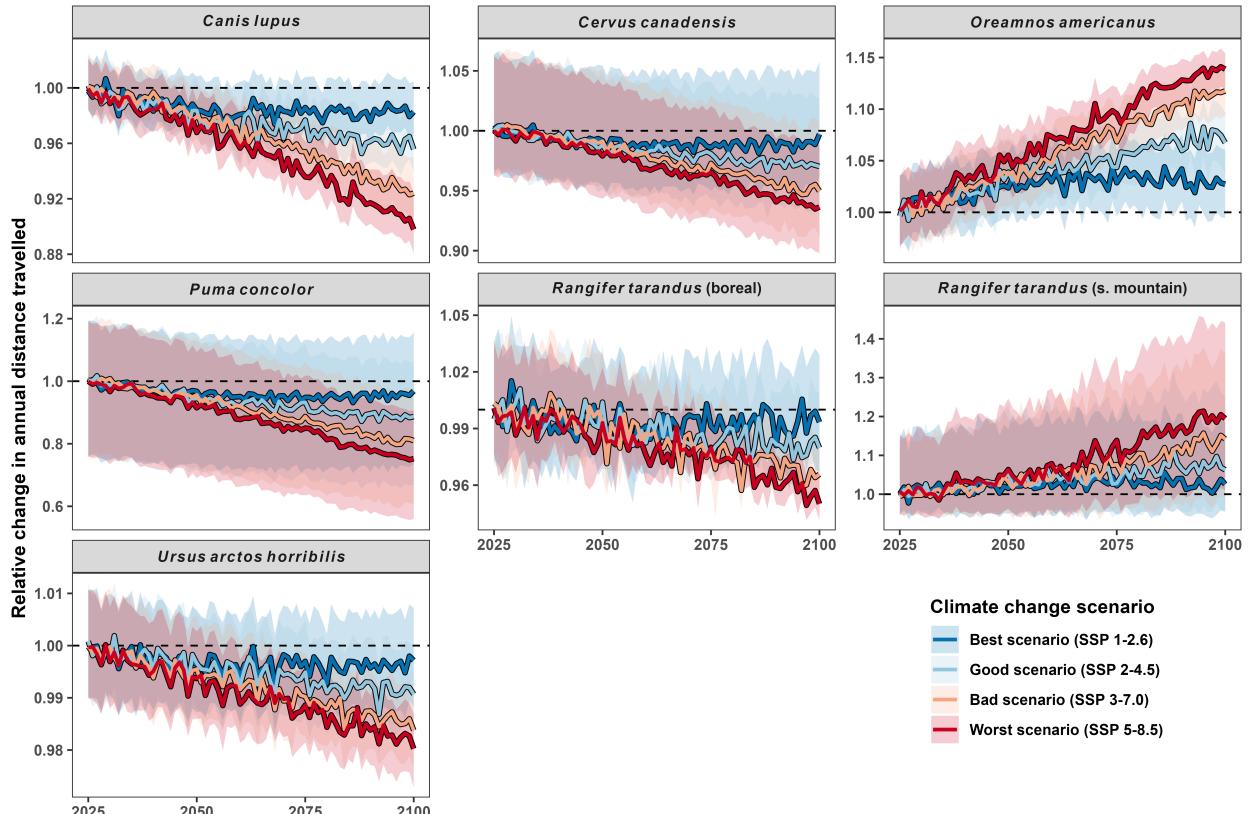


Figure 4: The direction and magnitude of changes in movement rates due to climate change varies among species, but worse climate-change scenarios result in the greatest change. Lines indicate the median projected change in distance travelled (probability of moving times speed when moving) due to changes in temperature within the species' current extent. Shaded areas indicate the 90% prediction interval within the range. Changes are relative to the predicted mean distances travelled in 2025 across the four Shared Socioeconomic Pathways (SSPs). The projections only account for changes in movement behaviour (i.e., movement frequency and speed) and ignore changes in physiology or movement costs.

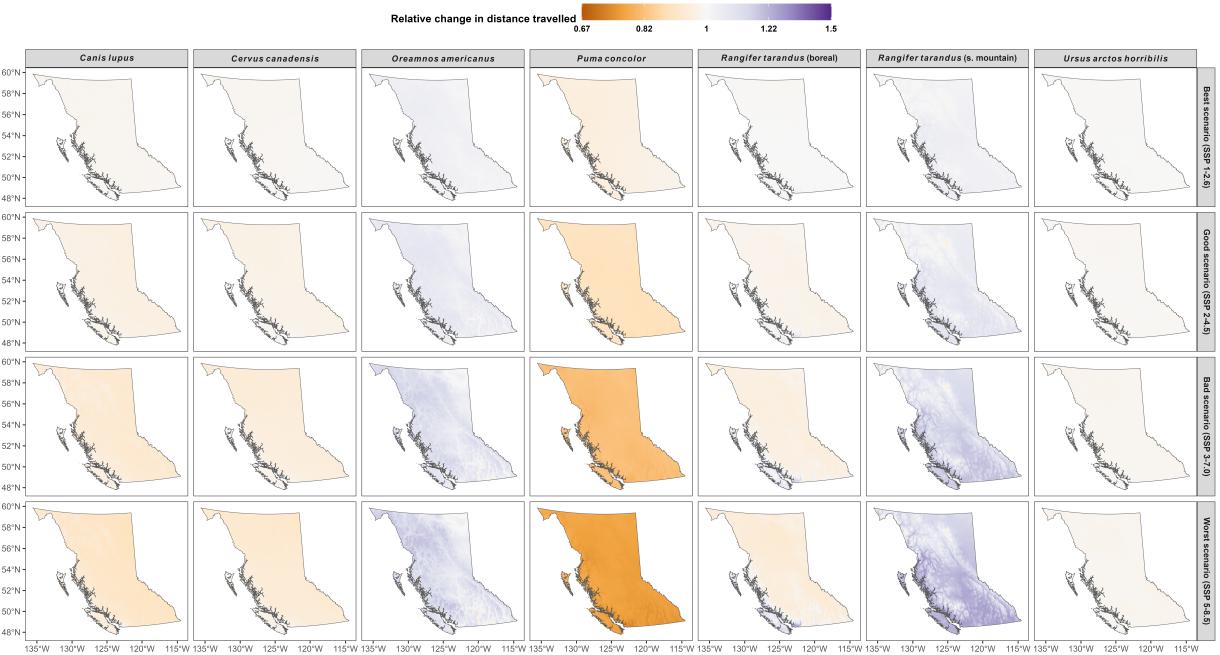


Figure 5: Climate change will impact each species' movement rates differently. The color scale indicates the predicted changes in distance traveled in 2100, relative to each location's average distance in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease, and values > 1 indicate an increase. For ease of readability, the color bar is on the \log_2 scale to help visualize patterns in doubling, and values are capped to 0.67 and 1.5 ($\approx 2^{\pm 0.585}$; original data ranged 0.72 to 1.29). The predictions only account for the predicted temperature throughout the province and ignore environmental factors such as terrain slope, soil type, and forest cover.

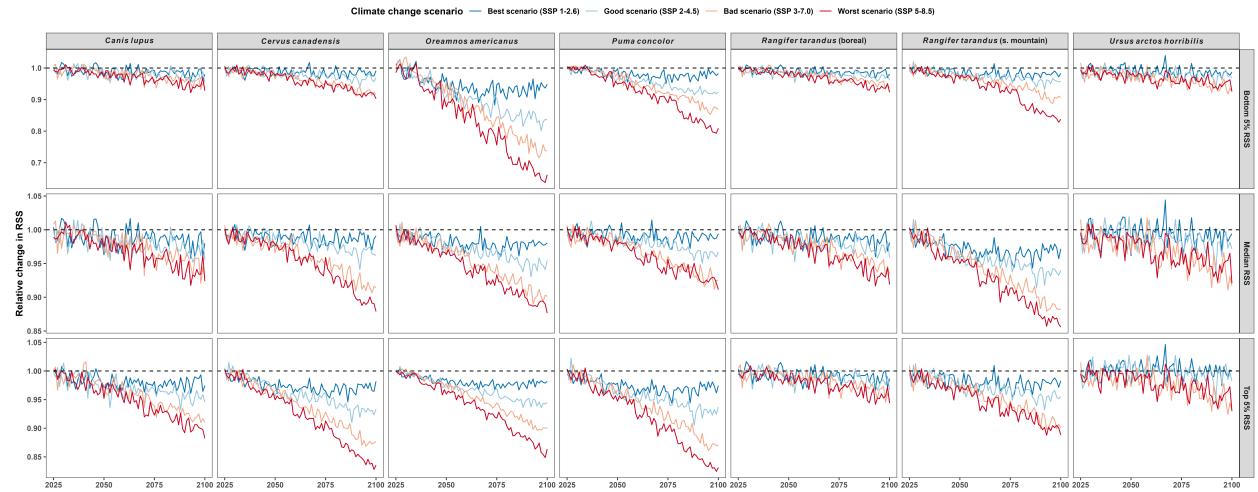


Figure 6: All species are expected to exhibit a decrease in relative selection strength (RSS) for their current range, irrespective of RSS quantile or climate change scenario, but decreases are stronger in the worse-case scenario. Lines indicate the projected change in RSS for the bottom 5%, median,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

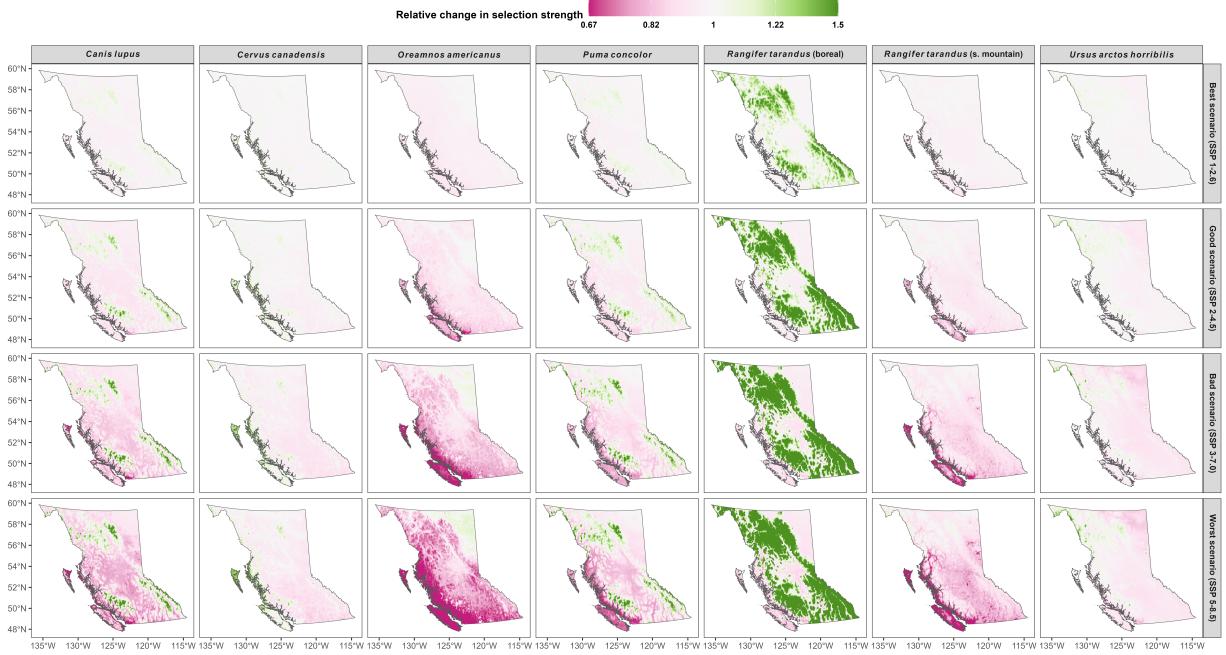


Figure 7: Climate change will impact each species’ habitat relative selection strength (RSS) differently. The color scale indicates the predicted changes in RSS in 2100, relative to each location’s average RSS in 2025 across all four scenarios, such that 1 indicates no change, values < 1 indicate a decrease,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

290 4 Discussion

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

303 prolonged [38,83], mammals will be increasingly forced towards atypical behaviours that
304 may alter community structures and behaviours, both during such events and afterwards
305 [55,84,85]. For instance, changes in climate and phenology impact the life history and be-
306 haviour of many hibernating mammals [86], and hot weather can also affects mammals'
307 sleep quality [87] and likelihood to enter torpor [88]. Such changes may alter the frequency
308 and intensity of human-wildlife conflict, especially with the addition of growing pressures
309 from human development and presence [30,43,89]. At the same time, warmer winters may
310 reduce mammals' energetic expenditure [32,90], increase ease of movement as snow cover
311 and depth decrease [14,15], increase their chances of finding food or being predated upon
312 [91–95], and affect the timing and duration of migrations [14,37,44]. These changes will
313 likely have complex consequences for population and ecosystem structures and dynamics as
314 prey, predators, and competitors experience altered seasonal cycles and increasingly common
315 climate “weirding” [42].

316 Our ability to respond to current and future changes in climate is contingent on our
317 ability to prepare for and predict change. However, predicting animal behaviour becomes
318 increasingly complicated as the conditions animals are exposed to deviate from current, typ-
319 ical conditions, especially when responses are nonlinear and data are sparse. Consequently,
320 we do not present our results as a definitive guide to how mammals in BC will respond
321 to climate change. Instead, we hope they serve as a starting point to (1) demonstrate that
322 mammals' movement rates and habitat selection depend on temperature and (2) how one can
323 estimate mammals' changes in movement behaviour due to climate change. Additionally,
324 communicating uncertainty in one's estimates is crucial in assessing risk probabilistically
325 [96–98]. Recent events in global politics, including global conflicts [99,100] and the rapid
326 rise in generative machine learning [more commonly: “AI,” see 101,102,103] and its pro-
327 hibitive energy and water demands [104] and carbon footprint [105], have placed doubt on
328 the feasibility of reaching climate change goals that seemed achievable in the past decade
329 [106]. Mitigating climate change and its consequences will require extensive and widespread

330 collaborative effort [107]. Similarly, protecting a third of the world’s ecosystems [Section H,
331 Targets 2 and 3 of 56] appears less tangible as global political and environmental conditions
332 change rapidly and unpredictably [43,108–110]. Achieving the “30 by 30” goal will require ac-
333 tive partnership with local Peoples, especially Indigenous Peoples [111,112]. Understanding
334 the consequences of climate change on mammals’ movement behaviour and spatial distri-
335 bution is a first step towards anticipating and proactively responding to future changes in
336 human-induced rapid environmental change [43,49]. In the following sections, we discuss the
337 implications of our results in more detail. We then expand on consequences for conservation
338 during the 21st century and considerations for future studies.

339 4.1 Effects of temperature on movement rates

340 The lack of common effects of temperature across all species’ movement rates indicates that
341 preparing for future changes will require a variety of physiological and behavioral adaptations
342 as ecological communities respond in complex and interconnected ways. Although our models
343 do not account for explicit physiological or phenological changes, the tensor product terms in
344 Fig. 2 suggest that warmer temperatures cause many species to alter their daily and seasonal
345 activity patterns (most visible in pumas and grizzly bears). For example, when temperatures
346 were above 0°C, pumas moved most at night, but when temperatures were below 0°C they
347 tended to move more throughout the day. Throughout the year, they adapted their tolerance
348 to temperature and moved less when it was relatively hot (for a given time of year), especially
349 in spring and summer. The strong reduction in the mid-day movement rates of wolves, elk,
350 pumas, and boreal caribou when summer temperatures were above 20°C suggests that the
351 increasingly common and intense heat waves across British Columbia will have community-
352 wide impacts on movement rates, encounter rates, and potentially community structure [29].
353 More work is necessary on quantifying interspecific responses to temperature, including the
354 effects of temperature on predation rates [but see: 113,114,115]. The increase in intensity
355 and frequency of extreme heat events [42,83] will likely also impact the occurrence and timing

356 of hibernation [86] and migration or seasonal range expansions [116–118]. However, not all
357 species may be able to adapt at the current rate of climate change [16,49], especially since
358 landscape changes will likely depend not only on the direct effect of temperature but also on
359 cascading changes in the availability and unpredictability of resources [28,119,120].

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

361 As with the effects of temperature on movement rates, the lack of common effects of
362 temperature across all species indicates that efficient and proactive habitat conservation
363 will require taxonomic nuance. In particular, our HRSFs did not account for any explicit
364 physiological responses to temperature that may impact movement, such as changes in the
365 phenology of plants, ice, or mammalian physiology or behaviour (e.g., moulting, migration),
366 other than as direct responses to temperature. Consequently, the behavioural changes we
367 present should be interpreted carefully. While some seasonal cycles do not depend directly
368 on temperature and may thus not be impacted directly by climate change [such as those
369 driven by photoperiod, see 121], the predictions we present also rely on the assumption
370 that mammals will not adapt these seasonal cycles to temperature-dependent cues, such
371 as weather [122] or forage availability [123], which may not be correct. Additionally, it is
372 important to stress the distinction between habitat selection and quality. While animals tend
373 to select for high-quality habitats [3,124], high selection strength can also be a consequence
374 of an ecological trap [125,126].

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

376 Achieving the goals laid out by the “30 by 30” conservation initiative [Section H, Tar-
377 gets 2 and 3 of 56] will require careful planning but often also rapid action. In the case
378 of Canada, only 13.7% of its terrestrial areas and inland waters were protected at the end
379 of 2023 [127,128]. Additionally, efficient and effective conservation will require collabora-
380 tion with Indigenous and local communities to ensure Treaties are respected in the process

[52,111,112,e.g., 129] while also actively preparing for future change [130,131]. The large range in predicted changes by 2100 (both across species and within species' current ranges) and high spatial heterogeneity in Fig. 7 highlight the need for careful planning that incorporates not only reliable estimates of change but also pragmatic and communicable measures of uncertainty and variability around such estimates. The width of the prediction intervals in Fig. 4 suggest that spatial and intra-individual variation should be accounted for when deciding the location and size of protected areas. Accurate estimates of the effects of changes in temperature on mammals' movement require a holistic view of the direct effects of temperature on mammals' movement directly as well as its effects on other drivers of movement, such as forage and prey availability [28], encounter rates [29,91], population dynamics [132], competitive pressure [133], and predation risk [134]. This complexity results in the great variation among the responses of different species (and individuals), especially as populations a rapid cascade of change [47] and animals face increasing pressures from human activity, including habitat fragmentation, habitat loss, and greater human presence in wild spaces [30,43,44,135–137]. As selection strength for current ranges changes (and likely decreases), some animals may disperse, relocate to a new habitat, or remain within the current range despite the reduced fitness and increased extinction risk [84,85,138].

4.4 Considerations for future studies

Our work highlights three central considerations for future research: (1) telemetry sampling rates should be designed primarily in relation to the movement timescales of the species of interest [71,139,140], (2) the number of individuals tracked and the length of each telemetry should depend not just on population size but also environmental stability, and (3) predicting changes in movement behaviour becomes highly complex when responses are non-linear, especially when changes depend on many interacting factors [35] and one is interested in predicting responses in extreme conditions for which data are scarce [141]. We address each consideration in the following three paragraphs.

407 While the `ctmm` models produced scale-independent estimates of speed [i.e., model inter-
408 pretation is independent of sampling interval: 71], the accuracy, size, and stability of speed
409 estimates still depended on the GPS sampling frequency. This is because coarsely-sampled
410 movement data contains information on large-scale movements (e.g., range crossings, mi-
411 grations) but not fine-scale movements [e.g., first-order habitat selection *sensu* 80, also see
412 139]. Using the boreal caribou as an example, the 13-hour sampling interval allows us to
413 reasonably estimate the caribou's movement path at a temporal scale of approximately 13
414 hours (or greater), but we cannot produce reasonable movement trajectories at a much finer
415 (e.g., hourly) scale. Consequently, we suggest being cautious when comparing estimated
416 movement behaviours across species, even though all predictions have been corrected to the
417 hourly timescale by predicting for 1-hour time intervals (i.e., `dt_hours = 1`). Thus, sampling
418 schedules should be fine enough to reconstruct animals' movement at a sufficiently fine scale.
419 Good estimates of an animal's speed and its movement path require telemetry locations to
420 be taken more often than the animal's directional persistence [71], so that, on average, the
421 dataset contains multiple locations in between changes in direction. What constitutes a
422 change in direction depends on what movement scale one is investigating. Small-scale move-
423 ments and first-order spatial selection will require more frequent sampling than migratory
424 movement or second- and third-order spatial selection. While `ctmm` movement models are
425 scale-invariant in that any model can be scaled to larger or smaller areas and timescales, the
426 model estimates are not independent of the scale of the sampling frequency.

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

434 carefully-designed sampling schedules and (Bayesian) hierarchical models can provide good
435 estimates of the effects of interested along with appropriate measures of uncertainty [98,142].

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

⁴⁴⁶ **References**

- ⁴⁴⁷ 1. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement
⁴⁴⁸ ecology paradigm for unifying organismal movement research. *Proceedings of the National
⁴⁴⁹ Academy of Sciences* [Internet]. 2008 [cited 2022 Mar 9];105:19052–9. Available from: <https://pnas.org/doi/full/10.1073/pnas.0800375105>
- ⁴⁵¹ 2. Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical Population
⁴⁵² Biology* [Internet]. 1976 [cited 2024 Jan 31];9:129–36. Available from: <https://linkinghub.elsevier.com/retrieve/pii/004058097690040X>
- ⁴⁵⁴ 3. Kacelnik A, Krebs JR, Bernstein C. The ideal free distribution and predator-prey popula-
⁴⁵⁵ tions. *Trends in Ecology & Evolution* [Internet]. 1992 [cited 2024 Jan 31];7:50–5. Available
⁴⁵⁶ from: <https://linkinghub.elsevier.com/retrieve/pii/016953479290106L>
- ⁴⁵⁷ 4. Winter VA, Smith BJ, Berger DJ, Hart RB, Huang J, Manlove K, et al. Forecasting
⁴⁵⁸ animal distribution through individual habitat selection: Insights for population inference
⁴⁵⁹ and transferable predictions. *Ecography* [Internet]. 2024 [cited 2024 Oct 9];e07225. Available
⁴⁶⁰ from: <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.07225>
- ⁴⁶¹ 5. Peterson AN, Soto AP, McHenry MJ. Pursuit and Evasion Strategies in the Predator–Prey
⁴⁶² Interactions of Fishes. *Integrative and Comparative Biology* [Internet]. 2021 [cited 2025 Jan
⁴⁶³ 15];61:668–80. Available from: <https://academic.oup.com/icb/article/61/2/668/6290712>
- 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 [Inter-
470 net]. 2024 [cited 2025 Jan 15];99:778–96. Available from: <https://onlinelibrary.wiley.com/>
471 doi/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->
475 Energetics-of-Temperature

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->
480 and-mechanics-of-terrestrial-locomotion

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>

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 from:
487 <http://climatechangeresponses.biomedcentral.com/articles/10.1186/s40665-016-0024-1>

488 12. Jahn M, Seebacher F. Variations in cost of transport and their ecological conse-
489 quences: A review. *Journal of Experimental Biology* [Internet]. 2022 [cited 2025 Jan
490 15];225:jeb243646. Available from: <https://journals.biologists.com/jeb/article/225/15/jeb243646/276242/Variations-in-cost-of-transport-and-their>

492 13. Montgomery RA, Redilla KM, Moll RJ, Van Moorter B, Rolandsen CM, Millspaugh
493 JJ, et al. Movement modeling reveals the complex nature of the response of moose to am-
494 bient temperatures during summer. *Journal of Mammalogy* [Internet]. 2019 [cited 2024
495 Aug 8];100:169–77. Available from: <https://academic.oup.com/jmammal/article/100/1/169/5299335>

497 14. Leclerc M, Leblond M, Le Corre M, Dussault C, Côté SD. Determinants of migration
498 trajectory and movement rate in a long-distance terrestrial mammal. Reyna R, editor.
499 *Journal of Mammalogy* [Internet]. 2021 [cited 2024 Jul 18];102:1342–52. Available from:
500 <https://academic.oup.com/jmammal/article/102/5/1342/6327749>

501 15. Melin M, Matala J, Mehtätalo L, Pusenius J, Packalen T. The effect of snow depth on
502 movement rates of GPS-collared moose. *European Journal of Wildlife Research* [Internet].
503 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>

508 17. Dyer A, Brose U, Berti E, Rosenbaum B, Hirt MR. The travel speeds of large animals are
509 limited by their heat-dissipation capacities. Hedenstrom A, editor. *PLOS Biology* [Internet].

510 2023 [cited 2024 Jun 10];21:e3001820. Available from: <https://dx.plos.org/10.1371/journal.pbio.3001820>

512 18. Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM. Fine-grain
513 modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia.
514 Trends in Ecology & Evolution [Internet]. 2014 [cited 2025 May 9];29:390–7. Available from:
515 <https://linkinghub.elsevier.com/retrieve/pii/S0169534714001001>

516 19. Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, et al.
517 Implications of the thermal environment for terrestrial wildlife management. Wildlife Society
518 Bulletin [Internet]. 2017 [cited 2024 Aug 8];41:183–93. Available from: <https://wildlife.onlinelibrary.wiley.com/doi/10.1002/wsb.772>

520 20. Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G. Effects of air temperature
521 on habitat selection and activity patterns of two tropical imperfect homeotherms. Ani-
522 mal Behaviour [Internet]. 2018 [cited 2024 Jun 10];140:129–40. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347218301209>

524 21. Arechavala-Lopez P, Minguito-Frutos M, Follana-Berná G, Palmer M. Common octopus
525 settled in human-altered Mediterranean coastal waters: From individual home range to
526 population dynamics. Durif C, editor. ICES Journal of Marine Science [Internet]. 2019
527 [cited 2022 Nov 7];76:585–97. Available from: <https://academic.oup.com/icesjms/article/76/2/585/4917675>

529 22. Gulland FMD, Baker JD, Howe M, LaBrecque E, Leach L, Moore SE, et al. A review
530 of climate change effects on marine mammals in United States waters: Past predictions,
531 observed impacts, current research and conservation imperatives. Climate Change Ecology

532 [Internet]. 2022 [cited 2025 May 9];3:100054. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2666900522000077>

534 23. Hall LE, Chalfoun AD, Beever EA, Loosen AE. Microrefuges and the occurrence of
535 thermal specialists: Implications for wildlife persistence amidst changing temperatures. Cli-
536 mate Change Responses [Internet]. 2016 [cited 2025 May 9];3:8. Available from: <http://climatechangeresponses.biomedcentral.com/articles/10.1186/s40665-016-0021-4>

538 24. Hegel TM, Mysterud A, Huettmann F, Stenseth NC. Interacting effect of wolves and
539 climate on recruitment in a northern mountain caribou population. Oikos [Internet]. 2010
540 [cited 2024 Aug 8];119:1453–61. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1600-0706.2010.18358.x>

542 25. Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, et al.
543 Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society
544 B: Biological Sciences [Internet]. 2016 [cited 2024 Feb 14];283:20160456. Available from:
545 <https://royalsocietypublishing.org/doi/10.1098/rspb.2016.0456>

546 26. Alston JM, Joyce MJ, Merkle JA, Moen RA. Temperature shapes movement and habitat
547 selection by a heat-sensitive ungulate. Landscape Ecology [Internet]. 2020 [cited 2022 Nov
548 18];35:1961–73. Available from: <https://link.springer.com/10.1007/s10980-020-01072-y>

549 27. Giroux A, Ortega Z, Attias N, Desbiez ALJ, Valle D, Börger L, et al. Activity mod-
550 ulation and selection for forests help giant anteaters to cope with temperature changes.
551 Animal Behaviour [Internet]. 2023 [cited 2024 Jun 10];201:191–209. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S000334722300101X>

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

- 576 34. McCain CM. Assessing the risks to United States and Canadian mammals caused by
577 climate change using a trait-mediated model. Heske E, editor. *Journal of Mammalogy*
578 [Internet]. 2019 [cited 2024 Jul 18];gyz155. Available from: <https://academic.oup.com/jmammal/advance-article/doi/10.1093/jmammal/gyz155/5614284>
- 580 35. Polazzo F, Limberger R, Pennekamp F, Ross SRP-J, Simpson GL, Petchey OL. Mea-
581 suring the Response Diversity of Ecological Communities Experiencing Multifarious Envi-
582 ronmental Change. *Global Change Biology* [Internet]. 2024 [cited 2025 Jan 16];30:e17594.
583 Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.17594>
- 584 36. Levins RA. Evolution in changing environments: Some theoretical explorations. 3.
585 printing. Princeton, NJ: Princeton Univ. Press; 1974.
- 586 37. Xu W, Barker K, Shawler A, Van Scoyoc A, Smith JA, Mueller T, et al. The plastic-
587 ity of ungulate migration in a changing world. *Ecology* [Internet]. 2021 [cited 2025 Jan
588 16];102:e03293. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3293>
- 589 38. IPCC. Climate Change 2021 – The Physical Science Basis: Working Group I Contri-
590 bution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change
591 [Internet]. 1st ed. Cambridge University Press; 2023 [cited 2023 Jun 30]. Available from:
592 <https://www.cambridge.org/core/product/identifier/9781009157896/type/book>
- 594 39. Zurowski M. The summer Canada burned: The wildfire season that shocked the world.
595 Vancouver: Postmedia / Greystone Books; 2023.

- 596 40. Deb JC, Forbes G, MacLean DA. Modelling the spatial distribution of selected North
597 American woodland mammals under future climate scenarios. *Mammal Review* [Internet].
598 2020 [cited 2024 Jun 13];50:440–52. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/mam.12210>
- 600 41. Woo-Durand C, Matte J-M, Cuddihy G, McGourdji CL, Venter O, Grant JWA. In-
601 creasing importance of climate change and other threats to at-risk species in Canada. *En-*
602 *vironmental Reviews* [Internet]. 2020 [cited 2022 Jun 23];28:449–56. Available from: <https://cdnsciencepub.com/doi/10.1139/er-2020-0032>
- 604 42. Bunnell FL, Kremsater LL, Wells RW. Global Weirding in British Columbia: Climate
605 Change and the Habitat of Terrestrial Vertebrates. *Journal of Ecosystems and Management*
606 [Internet]. 2011 [cited 2024 Jun 14];12. Available from: <https://jem-online.org/index.php/jem/article/view/74>
- 608 43. Sih A, Ferrari MCO, Harris DJ. Evolution and behavioural responses to human-induced
609 rapid environmental change: Behaviour and evolution. *Evolutionary Applications* [Internet].
610 2011 [cited 2022 Oct 5];4:367–87. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1752-4571.2010.00166.x>
- 612 44. Sawyer H, Kauffman MJ, Nielson RM, Horne JS. Identifying and prioritizing ungulate
613 migration routes for landscape-level conservation. *Ecological Applications* [Internet]. 2009
614 [cited 2025 Jan 16];19:2016–25. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-2034.1>
- 616 45. Verzuh TL, Rogers SA, Mathewson PD, May A, Porter WP, Class C, et al. Behavioural
617 responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales.

- 618 Journal of Animal Ecology [Internet]. 2023 [cited 2024 Jun 12];92:619–34. Available from:
619 <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13873>
- 620 46. Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL. Migratory plas-
621 ticity is not ubiquitous among large herbivores. Chapman J, editor. Journal of Animal
622 Ecology [Internet]. 2019 [cited 2025 Jan 16];88:450–60. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12926>
- 624 47. Botero CA, Weissing FJ, Wright J, Rubenstein DR. Evolutionary tipping points in the
625 capacity to adapt to environmental change. Proceedings of the National Academy of Sciences
626 [Internet]. 2015 [cited 2025 Feb 24];112:184–9. Available from: <https://pnas.org/doi/full/10.1073/pnas.1408589111>
- 628 48. Sherwood SC, Huber M. An adaptability limit to climate change due to heat stress. Pro-
629 ceedings of the National Academy of Sciences [Internet]. 2010 [cited 2024 Jun 14];107:9552–5.
630 Available from: <https://pnas.org/doi/full/10.1073/pnas.0913352107>
- 631 49. Williams JE, Blois JL. Range shifts in response to past and future climate change: Can
632 climate velocities and species' dispersal capabilities explain variation in mammalian range
633 shifts? Journal of Biogeography [Internet]. 2018 [cited 2024 Jul 18];45:2175–89. Available
634 from: <https://onlinelibrary.wiley.com/doi/10.1111/jbi.13395>
- 635 50. Mota-Rojas D, Titto CG, Orihuela A, Martínez-Burnes J, Gómez-Prado J, Torres-
636 Bernal F, et al. Physiological and Behavioral Mechanisms of Thermoregulation in Mammals.
637 Animals [Internet]. 2021 [cited 2024 Jun 12];11:1733. Available from: <https://www.mdpi.com/2076-2615/11/6/1733>

- 639 51. Dierauer JR, Allen DM, Whitfield PH. Climate change impacts on snow and streamflow
640 drought regimes in four ecoregions of British Columbia. Canadian Water Resources Journal
641 / Revue canadienne des ressources hydriques [Internet]. 2021 [cited 2025 Jan 16];46:168–93.
642 Available from: <https://www.tandfonline.com/doi/full/10.1080/07011784.2021.1960894>
- 643 52. Turner NJ, Clifton H. “It’s so different today”: Climate change and indigenous
644 lifeways in British Columbia, Canada. Global Environmental Change [Internet]. 2009
645 [cited 2025 Feb 20];19:180–90. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0959378009000223>
- 647 53. Tysor CS. Countergradient variation in lodgepole pine flowering phenology. 2025 [cited
648 2025 Feb 20]; Available from: <https://doi.library.ubc.ca/10.14288/1.0447901>
- 649 54. Basu A, Culpepper J, Blagrave K, Sharma S. Phenological Shifts in Lake Ice Cover Across
650 the Northern Hemisphere: A Glimpse Into the Past, Present, and the Future of Lake Ice Phe-
651 nology. Water Resources Research [Internet]. 2024 [cited 2025 Feb 20];60:e2023WR036392.
652 Available from: <https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2023WR036392>
- 653 55. Zhang X, Zhou T, Zhang W, Ren L, Jiang J, Hu S, et al. Increased impact of heat domes
654 on 2021-like heat extremes in North America under global warming. Nature Communications
655 [Internet]. 2023 [cited 2025 Jan 21];14:1690. Available from: <https://www.nature.com/articles/s41467-023-37309-y>
- 657 56. Convention on Biological Diversity. 15/4. Kunming-Montreal Global Biodiversity
658 Framework [Internet]. 2022 [cited 2025 Jan 16]. Available from: <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>

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

- 682 63. Burnett M. climatenaR: Tools to Access ClimateNA data. 2023.
- 683 64. Rigby RA, Stasinopoulos DM. Generalized additive models for location, scale and shape
684 (with discussion). Journal of the Royal Statistical Society: Series C (Applied Statistics)
685 [Internet]. 2005 [cited 2022 Jun 26];54:507–54. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.1467-9876.2005.00510.x>
- 686 65. Stasinopoulos MD, Rigby RA. Generalized additive models for location scale and shape
687 (GAMLSS) in R. Journal of Statistical Software. 2007;23.
- 688 66. Wood SN. Generalized additive models: An introduction with R. Second edition. Boca
689 Raton: CRC Press/Taylor & Francis Group; 2017.
- 690 67. Tuanmu M, Jetz W. A global 1-km consensus land-cover product for biodiversity and
691 ecosystem modelling. Global Ecology and Biogeography [Internet]. 2014 [cited 2025 Jan
692 17];23:1031–45. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/geb.12182>
- 693 68. Hollister J, Shah T, Nowosad J, Robitaille AL, Beck MW, Johnson M. Elevatr: Access
694 Elevation Data from Various APIs [Internet]. 2023. Available from: <https://github.com/jhollist/elevatr/>
- 695 69. Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. From Fine-
696 Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes
697 across Spatiotemporal Scales. The American Naturalist [Internet]. 2014 [cited 2022 Jul
698 26];183:E154–67. Available from: <https://www.journals.uchicago.edu/doi/10.1086/675504>
- 700 70. Fleming CH, Calabrese JM. Ctmm: Continuous-Time Movement Modeling [Internet].

- 702 2023. Available from: <https://CRAN.R-project.org/package=ctmm>
- 703 71. Noonan MJ, Fleming CH, Akre TS, Drescher-Lehman J, Gurarie E, Harrison A-L,
704 et al. Scale-insensitive estimation of speed and distance traveled from animal tracking
705 data. Movement Ecology [Internet]. 2019 [cited 2021 Jun 23];7:35. Available from: <https:////movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-019-0177-1>
- 706
- 707 72. Matthiopoulos J. Defining, estimating, and understanding the fundamental niches of
708 complex animals in heterogeneous environments. Ecological Monographs [Internet]. 2022
709 [cited 2025 Jan 17];92:e1545. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecm.1545>
- 710
- 711 73. Pedersen EJ, Miller DL, Simpson GL, Ross N. Hierarchical generalized additive models
712 in ecology: An introduction with mgcv. PeerJ [Internet]. 2019 [cited 2020 Jan 24];7:e6876.
713 Available from: <https://peerj.com/articles/6876>
- 714
- 715 74. Wood SN, Goude Y, Shaw S. Generalized additive models for large data sets. Journal of
716 the Royal Statistical Society: Series C (Applied Statistics) [Internet]. 2015 [cited 2022 Mar
717 11];64:139–55. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/rssc.12068>
- 718
- 719 75. Wood SN, Li Z, Shaddick G, Augustin NH. Generalized Additive Models for Gigadata:
720 Modeling the U.K. Black Smoke Network Daily Data. Journal of the American Statistical
721 Association [Internet]. 2017 [cited 2022 Mar 11];112:1199–210. Available from: <https://www.tandfonline.com/doi/full/10.1080/01621459.2016.1195744>
- 722
- 723 76. Li Z, Wood SN. Faster model matrix crossproducts for large generalized linear models
724 with discretized covariates. Statistics and Computing [Internet]. 2020;30:19–25. Available

723 from: <https://doi.org/10.1007/s11222-019-09864-2>

724 77. Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J. Estimating space-use
725 and habitat preference from wildlife telemetry data. *Ecography* [Internet]. 2008 [cited 2023
726 Jun 22];31:140–60. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/j.2007.0906-7590.05236.x>

728 78. Fleming CH, Calabrese JM. A new kernel density estimator for accurate home-range and
729 species-range area estimation. Dray S, editor. *Methods in Ecology and Evolution* [Internet].
730 2017 [cited 2025 Jan 17];8:571–9. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.12673>

732 79. Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, et al. A comprehen-
733 sive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*
734 [Internet]. 2019 [cited 2020 Oct 23];89:e01344. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1344>

736 80. Johnson DH. The Comparison of Usage and Availability Measurements for Evaluating
737 Resource Preference. *Ecology* [Internet]. 1980 [cited 2025 Jan 17];61:65–71. Available from:
738 <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1937156>

739 81. Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, et al. Mitigat-
740 ing pseudoreplication and bias in resource selection functions with autocorrelation-informed
741 weighting. *Methods in Ecology and Evolution* [Internet]. 2022 [cited 2022 Dec 12];2041–
742 210X.14025. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/2041-210X.14025>

743 82. Akaike H. A new look at the statistical model identification. *IEEE Transactions on*

- ⁷⁴⁴ Automatic Control [Internet]. 1974 [cited 2022 Dec 28];19:716–23. Available from: <http://ieeexplore.ieee.org/document/1100705/>
- ⁷⁴⁵
- ⁷⁴⁶ 83. Yao Q, Fan J, Meng J, Lucarini V, Jensen HJ, Christensen K, et al. Emergence of
⁷⁴⁷ universal scaling in weather extreme events. 2022 [cited 2022 Nov 20]; Available from:
⁷⁴⁸ <https://arxiv.org/abs/2209.02292>
- ⁷⁴⁹ 84. Logares R, Nuñez M. Black Swans in ecology and evolution: The importance of improba-
⁷⁵⁰ ble but highly influential events. Ideas in Ecology and Evolution [Internet]. 2012 [cited 2020
⁷⁵¹ Feb 12]; Available from: <https://ojs.library.queensu.ca/index.php/IEE/article/view/4311>
- ⁷⁵² 85. Anderson SC, Branch TA, Cooper AB, Dulvy NK. Black-swan events in animal
⁷⁵³ populations. Proceedings of the National Academy of Sciences [Internet]. 2017 [cited
⁷⁵⁴ 2020 Jan 24];114:3252–7. Available from: <http://www.pnas.org/lookup/doi/10.1073/pnas.1611525114>
- ⁷⁵⁵
- ⁷⁵⁶ 86. Wells CP, Barbier R, Nelson S, Kanaziz R, Aubry LM. Life history consequences of cli-
⁷⁵⁷ mate change in hibernating mammals: A review. Ecography [Internet]. 2022 [cited 2025 Jan
⁷⁵⁸ 21];2022:e06056. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.06056>
- ⁷⁵⁹ 87. Mortlock E, Silovský V, Güldenpfennig J, Faltusová M, Olejarz A, Börger L, et al. Sleep
⁷⁶⁰ in the wild: The importance of individual effects and environmental conditions on sleep
⁷⁶¹ behaviour in wild boar. Proceedings of the Royal Society B: Biological Sciences [Internet].
⁷⁶² 2024 [cited 2025 Jan 21];291:20232115. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2023.2115>
- ⁷⁶³
- ⁷⁶⁴ 88. Fjelldal MA, Wright J, Stawski C. Nightly torpor use in response to weather conditions

⁷⁶⁵ and individual state in an insectivorous bat. *Oecologia* [Internet]. 2021 [cited 2022 Oct
⁷⁶⁶ 3];197:129–42. Available from: <https://link.springer.com/10.1007/s00442-021-05022-6>

⁷⁶⁷ 89. Johnson HE, Lewis DL, Verzuh TL, Wallace CF, Much RM, Willmarth LK, et al.
⁷⁶⁸ Human development and climate affect hibernation in a large carnivore with implications
⁷⁶⁹ for human–carnivore conflicts. Bieber C, editor. *Journal of Applied Ecology* [Internet]. 2018
⁷⁷⁰ [cited 2025 Jan 21];55:663–72. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.13021>

⁷⁷² 90. Schmidt NM, Grøndahl C, Evans AL, Desforges J-P, Blake J, Hansen LH, et al. On
⁷⁷³ the interplay between hypothermia and reproduction in a high arctic ungulate. *Scientific
Reports* [Internet]. 2020 [cited 2022 Sep 2];10:1514. Available from: <http://www.nature.com/articles/s41598-020-58298-8>

⁷⁷⁶ 91. Hou R, Chapman CA, Jay O, Guo S, Li B, Raubenheimer D. Cold and hungry: Combined
⁷⁷⁷ effects of low temperature and resource scarcity on an edge-of-range temperate primate,
⁷⁷⁸ the golden snub-nose monkey. *Ecography* [Internet]. 2020 [cited 2022 Oct 3];43:1672–82.
⁷⁷⁹ Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ecog.05295>

⁷⁸⁰ 92. Gilbert SL, Hundertmark KJ, Person DK, Lindberg MS, Boyce MS. Behavioral plasticity
⁷⁸¹ in a variable environment: Snow depth and habitat interactions drive deer movement in
⁷⁸² winter. *Journal of Mammalogy* [Internet]. 2017 [cited 2025 Jan 21];98:246–59. Available
⁷⁸³ from: <https://academic.oup.com/jmammal/article-lookup/doi/10.1093/jmammal/gyw167>

⁷⁸⁴ 93. Pedersen SH, Bentzen TW, Reinking AK, Liston GE, Elder K, Lenart EA, et al. Quantifying
⁷⁸⁵ effects of snow depth on caribou winter range selection and movement in Arctic
⁷⁸⁶ Alaska. *Movement Ecology* [Internet]. 2021 [cited 2025 Jan 21];9:48. Available from:

787 <https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-021-00276-4>

788 94. Slatyer RA, Umbers KDL, Arnold PA. Ecological responses to variation in seasonal snow
789 cover. *Conservation Biology* [Internet]. 2022 [cited 2025 Jan 21];36:e13727. Available from:
790 <https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13727>

791 95. Sullender BK, Cunningham CX, Lundquist JD, Prugh LR. Defining the danger zone:
792 Critical snow properties for predator–prey interactions. *Oikos* [Internet]. 2023 [cited 2025
793 Jan 21];2023:e09925. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.09925>

795 96. Aven T, Kvaløy JT. Implementing the Bayesian paradigm in risk analysis. *Reliability*
796 *Engineering & System Safety* [Internet]. 2002 [cited 2025 Jan 30];78:195–201. Available
797 from: <https://linkinghub.elsevier.com/retrieve/pii/S0951832002001618>

798 97. Ayre KK, Landis WG. A Bayesian Approach to Landscape Ecological Risk Assessment
799 Applied to the Upper Grande Ronde Watershed, Oregon. *Human and Ecological Risk As-*
800 *sessment: An International Journal* [Internet]. 2012 [cited 2025 Jan 30];18:946–70. Available
801 from: <http://www.tandfonline.com/doi/abs/10.1080/10807039.2012.707925>

802 98. Czado C, Brechmann EC. Bayesian Risk Analysis. In: Klüppelberg C, Straub D,
803 Welpe IM, editors. *Risk - A Multidisciplinary Introduction* [Internet]. Cham: Springer
804 International Publishing; 2014 [cited 2025 Jan 30]. p. 207–40. Available from: https://link.springer.com/10.1007/978-3-319-04486-6_8

806 99. McNutt M, Hildebrand J. Scientists in the line of fire. *Science* [Internet]. 2022 [cited 2025
807 Feb 11];375:1071–1. Available from: <https://www.science.org/doi/10.1126/science.abp8817>

- 808 100. Tollefson J. What the war in Ukraine means for energy, climate and food. *Nature*
809 [Internet]. 2022 [cited 2025 Feb 11];604:232–3. Available from: <https://www.nature.com/articles/d41586-022-00969-9>
- 811 101. Roumeliotis KI, Tselikas ND. ChatGPT and Open-AI Models: A Preliminary Review.
812 Future Internet [Internet]. 2023 [cited 2025 Feb 11];15:192. Available from: <https://www.mdpi.com/1999-5903/15/6/192>
- 814 102. Van Noorden R, Webb R. ChatGPT and science: The AI system was a force in 2023
815 — for good and bad. *Nature* [Internet]. 2023 [cited 2025 Feb 11];624:509–9. Available from:
816 <https://www.nature.com/articles/d41586-023-03930-6>
- 817 103. DeepSeek-AI, Guo D, Yang D, Zhang H, Song J, Zhang R, et al. DeepSeek-R1:
818 Incentivizing Reasoning Capability in LLMs via Reinforcement Learning [Internet]. arXiv;
819 2025 [cited 2025 Jan 30]. Available from: <https://arxiv.org/abs/2501.12948>
- 820 104. Li P, Yang J, Islam MA, Ren S. Making AI Less "Thirsty": Uncovering and Addressing
821 the Secret Water Footprint of AI Models [Internet]. arXiv; 2023 [cited 2025 Jan 16]. Available
822 from: <https://arxiv.org/abs/2304.03271>
- 823 105. Luccioni AS, Viguier S, Ligozat A-L. Estimating the carbon footprint of BLOOM, a
824 176B parameter language model. *J Mach Learn Res.* 2024;24.
- 825 106. United Nations Environment Programme, Olhoff A, Bataille C, Christensen J, Den
826 Elzen M, Fransen T, et al. Emissions Gap Report 2024: No more hot air ... please! With a
827 massive gap between rhetoric and reality, countries draft new climate commitments [Inter-
828 net]. United Nations Environment Programme; 2024 [cited 2025 Jan 30]. Available from:

829 <https://wedocs.unep.org/20.500.11822/46404>

830 107. Huang M-T, Zhai P-M. Achieving Paris Agreement temperature goals requires carbon
831 neutrality by middle century with far-reaching transitions in the whole society. Advances
832 in Climate Change Research [Internet]. 2021 [cited 2025 Jan 30];12:281–6. Available from:
833 <https://linkinghub.elsevier.com/retrieve/pii/S1674927821000435>

834 108. Simmons BA, Nolte C, McGowan J. Tough questions for the “30 × 30” conserva-
835 tion agenda. Frontiers in Ecology and the Environment [Internet]. 2021 [cited 2025 Feb
836 11];19:322–3. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2375>

838 109. Guenette JD, Kenworthy PG, Wheeler CM. Implications of the War in Ukraine for the
839 Global Economy.<http://documents.worldbank.org/curated/en/099616504292238906>. Wash-
840 ington, D.C.: World Bank Group; 2022 Mar. Report No.: 3.

841 110. Sovacool BK, Baum C, Low S. The next climate war? Statecraft, security, and
842 weaponization in the geopolitics of a low-carbon future. Energy Strategy Reviews [Inter-
843 net]. 2023 [cited 2025 Feb 18];45:101031. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2211467X22002255>

845 111. Wong C, Ballegooien K, Ignace L, Johnson MJ(Gùdia), Swanson H. Towards reconcili-
846 ation: 10 Calls to Action to natural scientists working in Canada. Boran I, editor. FACETS
847 [Internet]. 2020 [cited 2021 Oct 27];5:769–83. Available from: <http://www.facetsjournal.com/doi/10.1139/facets-2020-0005>

849 112. Lamb CT, Willson R, Menzies AK, Owens-Beek N, Price M, McNay S, et al. Braiding

850 Indigenous rights and endangered species law. Science [Internet]. 2023 [cited 2023 Jul
851 19];380:694–6. Available from: <https://www.science.org/doi/10.1126/science.adg9830>

852 113. Cunningham SJ, Gardner JL, Martin RO. Opportunity costs and the response of birds
853 and mammals to climate warming. Frontiers in Ecology and the Environment [Internet].
854 2021 [cited 2025 Jan 30];19:300–7. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2324>

856 114. Glass TW, Breed GA, Robards MD, Williams CT, Kielland K. Trade-off between
857 predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted
858 mesocarnivore. Animal Behaviour [Internet]. 2021 [cited 2025 Jan 30];175:163–74. Available
859 from: <https://linkinghub.elsevier.com/retrieve/pii/S0003347221000658>

860 115. Brivio F, Apollonio M, Anderwald P, Filli F, Bassano B, Bertolucci C, et al. Seeking
861 temporal refugia to heat stress: Increasing nocturnal activity despite predation risk.
862 Proceedings of the Royal Society B: Biological Sciences [Internet]. 2024 [cited 2025 Jan
863 30];291:20231587. Available from: <https://royalsocietypublishing.org/doi/10.1098/rspb.2023.1587>

865 116. Carbeck K, Wang T, Reid JM, Arcese P. Adaptation to climate change through seasonal
866 migration revealed by climatic versus demographic niche models. Global Change Biology
867 [Internet]. 2022 [cited 2025 Feb 24];28:4260–75. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/gcb.16185>

869 117. Morley ID. Spatiotemporal analysis of ecosystem change and landscape connectivity
870 using satellite imagery in west-central British Columbia, Canada. 2021 [cited 2025 Feb 24];
871 Available from: <https://doi.library.ubc.ca/10.14288/1.0402358>

872 118. Malpeli KC. Ungulate migration in a changing climate—An initial assessment of climate
873 impacts, management priorities, and science needs [Internet]. Reston, VA; 2022 p. 32.
874 Report No.: 1493. Available from: <https://pubs.usgs.gov/publication/cir1493>

875 119. McLellan ML, McLellan BN. Effect of Season and High Ambient Temperature on
876 Activity Levels and Patterns of Grizzly Bears (*Ursus arctos*). Crocker DE, editor. PLOS
877 ONE [Internet]. 2015 [cited 2025 Mar 3];10:e0117734. Available from: <https://dx.plos.org/10.1371/journal.pone.0117734>

879 120. Pigeon KE, Stenhouse G, Côté SD. Drivers of hibernation: Linking food and weather
880 to denning behaviour of grizzly bears. Behavioral Ecology and Sociobiology [Internet]. 2016
881 [cited 2025 Mar 3];70:1745–54. Available from: <http://link.springer.com/10.1007/s00265-016-2180-5>

883 121. Liu JA, Meléndez-Fernández OH, Bumgarner JR, Nelson RJ. Effects of light pollu-
884 tion on photoperiod-driven seasonality. Hormones and Behavior [Internet]. 2022 [cited
885 2025 Feb 24];141:105150. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0018506X22000447>

887 122. Xu F, Si Y. The frost wave hypothesis: How the environment drives autumn departure
888 of migratory waterfowl. Ecological Indicators [Internet]. 2019 [cited 2025 Feb 24];101:1018–
889 25. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S1470160X19301335>

890 123. Middleton AD, Merkle JA, McWhirter DE, Cook JG, Cook RC, White PJ, et al. Green-
891 wave surfing increases fat gain in a migratory ungulate. Oikos [Internet]. 2018 [cited 2022
892 Sep 2];127:1060–8. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/oik.05227>

893 124. Wright CA. Survival and movements of mule deer (*Odocoileus hemionus*) in south-
894 ern British Columbia [Internet] [{PhD} {Thesis}]. University of British Columbia; 2024.
895 Available from: <https://open.library.ubc.ca/collections/ubctheses/24/items/1.0441418>

896 125. Zuñiga-Palacios J, Zuria I, Castellanos I, Lara C, Sánchez-Rojas G. What do we
897 know (and need to know) about the role of urban habitats as ecological traps? Sys-
898 tematic review and meta-analysis. *Science of The Total Environment* [Internet]. 2021
899 [cited 2025 Feb 24];780:146559. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0048969721016272>

901 126. Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R. An overview of
902 ecological traps in marine ecosystems. *Frontiers in Ecology and the Environment* [Internet].
903 2021 [cited 2025 Feb 24];19:234–42. Available from: <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/fee.2322>

905 127. Environment and Climate Change Canada. Canadian Environmental Sus-
906 tainability Indicators: Canada's conserved areas. [Internet]. 2024. Available from:
907 www.canada.ca/en/environment-climate-change/services/environmental-indicators/conserved-areas.html

909 128. Minister of Environment and Climate Change. An Act respecting transparency and
910 accountability in relation to certain commitments Canada has made under the Convention
911 on Biological Diversity [Internet]. 2024 [cited 2025 Feb 24]. Available from: <https://www.parl.ca/legisinfo/en/bill/44-1/c-73>

913 129. Falardeau M, Bennett EM, Else B, Fisk A, Mundy CJ, Choy ES, et al. Biophys-
914 ical indicators and Indigenous and Local Knowledge reveal climatic and ecological shifts

915 with implications for Arctic Char fisheries. *Global Environmental Change* [Internet]. 2022
916 [cited 2025 Feb 24];74:102469. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S0959378022000073>

918 130. Desjardins SPA, Friesen TM, Jordan PD. Looking back while moving forward: How
919 past responses to climate change can inform future adaptation and mitigation strategies
920 in the Arctic. *Quaternary International* [Internet]. 2020 [cited 2025 Feb 24];549:239–48.
921 Available from: <https://linkinghub.elsevier.com/retrieve/pii/S1040618220302822>

922 131. Hessami MA, Bowles E, Popp JN, Ford AT. Indigenizing the North American Model
923 of Wildlife Conservation. Beazley K, editor. *FACETS* [Internet]. 2021 [cited 2021 Nov
924 4];6:1285–306. Available from: <https://facetsjournal.com/doi/10.1139/facets-2020-0088>

925 132. Smith BJ, MacNulty DR, Stahler DR, Smith DW, Avgar T. Density-dependent habi-
926 tation selection alters drivers of population distribution in northern Yellowstone elk. *Ecology*
927 Letters [Internet]. 2023 [cited 2025 May 9];26:245–56. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/ele.14155>

929 133. Tórrez-Herrera LL, Davis GH, Crofoot MC. Do Monkeys Avoid Areas of Home Range
930 Overlap Because They Are Dangerous? A Test of the Risk Hypothesis in White-Faced
931 Capuchin Monkeys (*Cebus capucinus*). *International Journal of Primatology* [Internet]. 2020
932 [cited 2022 Mar 9];41:246–64. Available from: <http://link.springer.com/10.1007/s10764-019-00110-0>

934 134. Kohl MT, Ruth TK, Metz MC, Stahler DR, Smith DW, White PJ, et al. Do prey
935 select for vacant hunting domains to minimize a multi-predator threat? Gaillard J, editor.
936 *Ecology Letters* [Internet]. 2019 [cited 2025 Jan 20];22:1724–33. Available from: [https:](https://)

937 [//onlinelibrary.wiley.com/doi/10.1111/ele.13319](https://onlinelibrary.wiley.com/doi/10.1111/ele.13319)

938 135. Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC,
939 et al. Moving in the Anthropocene: Global reductions in terrestrial mammalian move-
940 ments. *Science* [Internet]. 2018 [cited 2020 Nov 11];359:466–9. Available from: <https://www.sciencemag.org/lookup/doi/10.1126/science.aam9712>

942 136. Rosenthal J, Booth R, Carolan N, Clarke O, Curnew J, Hammond C, et al. The impact
943 of recreational activities on species at risk in Canada. *Journal of Outdoor Recreation and*
944 *Tourism* [Internet]. 2022 [cited 2025 Feb 24];40:100567. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S2213078022000895>

946 137. Rice WL. The conspicuous consumption of wilderness, or leisure lost in the wilderness.
947 *World Leisure Journal* [Internet]. 2022 [cited 2025 Feb 24];64:451–68. Available from: <https://www.tandfonline.com/doi/full/10.1080/16078055.2022.2096109>

949 138. Duncan C, Chauvenet ALM, McRae LM, Pettorelli N. Predicting the Future Impact
950 of Droughts on Ungulate Populations in Arid and Semi-Arid Environments. Seebacher F,
951 editor. *PLoS ONE* [Internet]. 2012 [cited 2025 Feb 24];7:e51490. Available from: <https://dx.plos.org/10.1371/journal.pone.0051490>

953 139. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data ap-
954 proaches lead to an increased understanding of the ecology of animal movement. *Science*
955 [Internet]. 2022 [cited 2022 Mar 9];375:eabg1780. Available from: <https://www.science.org/doi/10.1126/science.abg1780>

957 140. Pease BS. Ecological scales of effect vary across space and time. *Ecography* [Inter-

⁹⁵⁸ net]. 2024 [cited 2024 Aug 8];2024:e07163. Available from: <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.07163>

⁹⁶⁰ 141. Steixner-Kumar S, Gläscher J. Strategies for navigating a dynamic world. Science
⁹⁶¹ [Internet]. 2020 [cited 2022 Mar 9];369:1056–7. Available from: <https://www.science.org/doi/10.1126/science.abd7258>

⁹⁶³ 142. McElreath R. Statistical rethinking: A Bayesian course with examples in R and Stan.
⁹⁶⁴ Second edition. Boca Raton London New York: CRC Press; 2020.